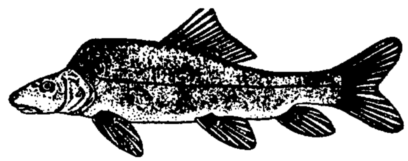
Biological Report 24
July 1994

Instream Flows to Assist the Recovery of Endangered Fishes of the Upper Colorado River Basin



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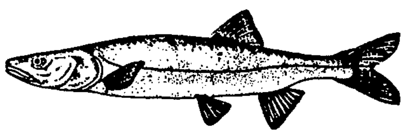
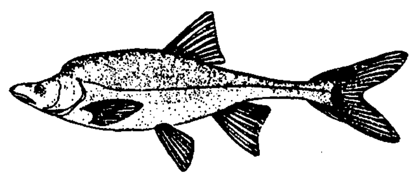
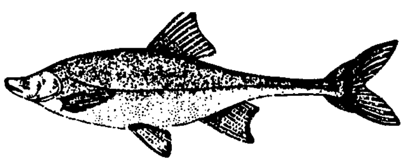


Colorado Squawfish



Humpback Chub



Bonytail Chub

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Instream Flows to Assist the Recovery of Endangered Fishes of the Upper Colorado River Basin

By

Jack A. Stanford

Patrick C. Nelson, Project Officer

U.S. Fish and Wildlife Service
P.O. Box 25486
Denver Federal Center
Denver, Colorado 80225

U.S. Department of the Interior
National Biological Survey
Washington, D.C. 20240

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by

Jack A. Stanford

Flathead Lake Biological Station
The University of Montana
311 Bio Station Lane
Polson, Montana 59860

Abstract. The riverine landscape of the Upper Colorado River Basin has been extensively modified by dams, diversions, revetments, and water abstractions. These changes, probably coupled with the introduction of many nonnative fishes, have compromised the existence of four of the native fishes (Colorado River squawfish *Ptychocheilus lucius*, humpback chub *Gila cypha*, bonytail chub *Gila elegans*, and razorback sucker *Xyrauchen texanus*) of the river system. Efforts to recover these endangered fishes have emphasized reregulation of flows to provide better habitat conditions than existed during the last half century, when ranges and abundances of the fishes declined significantly. Contention emerged, however, with regard to the efficacy of methods used by the U.S. Fish and Wildlife Service to justify flow recommendations to protect the endangered fishes. The purpose of this study was to review the science pertaining to the issue of flow provision, to identify critical uncertainties, and to provide recommendations for determining the instream flow needs of the endangered fishes.

Colorado River squawfish, humpback chub, and razorback sucker (in order of relative abundance; all are rare) live in the warm water (downstream) reaches of the Upper Colorado River Basin. Bonytail chub seem to be extirpated. Routine collections of larvae and age structure of populations in the Green and Colorado rivers indicate that adult recruitment of squawfish is occurring almost every year. Recruitment of adult humpback chub and razorback sucker has not been demonstrated, but both are known to produce young, at least in some years. Production of young squawfish seems to be lowest in years of very low or very high flows. However, studies strongly indicate that truncation of peak flows and higher, fluctuating baseflows (loss of seasonality) resulting from river regulation have altered complex biophysical processes that form and maintain low velocity habitats required for survival of the various life history stages of the fishes. An ecological tradeoff apparently exists: Very high flows are needed occasionally to produce habitats that the fish need to survive, but at the expense of reproductive success.

The apparent importance of variable, but clearly seasonal, flow regimes and associated biophysical interactions was the key rationale for the flow recommendations made by the U.S. Fish and Wildlife Service. For the Yampa, Green, and Colorado rivers, flows were recommended that would increase amplitude of the spring peak and reduce short-term fluctuations from hydropower operations at baseflows. However, on the Green River, the peak flows recommended for wet years were considerably less than flows of record and allowed substantial flow fluctuations during the late summer, fall, and winter (baseflow) period in all years. Moreover, a complex flow-habitat model was used to support flow recommendations on the Colorado River, but model output was discarded on the Green and Yampa rivers. Review of models currently used to determine an incremental relationship between flow and river conditions favorable to the endangered fishes revealed that none, including the one used on the Colorado River, was sufficiently well developed to be used exclusive of many other ecological measures. Inconsistencies in rationale and perceived need for a predictive model compromised the science that

strongly supported reregulation of flows in the Green and Colorado rivers to produce more natural, seasonal patterns.

Based on review of the ecological information and recognizing the problems in the methodological approaches that were used to derive flow recommendations, several key uncertainties seem to be critical to the goal of establishing flow regimes that will ultimately recover the endangered fishes.

- Flow seasonality and its correlates (e.g., temperature and physical habitat) may not be the factors limiting recovery of the native fishes.
- Given the high societal value placed on tailwater trout fisheries and the high priority placed on meeting entitlements under the Colorado River Compact and current water law, water volume in the Colorado and Green rivers may be insufficient to produce flows required to recover the fishes.
- Channel and floodplain morphology in time and space is not a simple flow-area relationship, and complex interactions not yet fully understood may emerge that will compromise recovery of the fish.
- What is the tradeoff between the propensity of endangered fish larvae to drift downstream and the need for high flows to maintain connectivity between the channel and backwaters and wetlands?
- Can food webs reestablish in key low velocity habitats (backwaters) to the extent needed to recover the fishes, given the windows permitted or needed for hydropower operations?
- Can the endangered fishes expand their range and productivity, given the downstream extension of coldwater environments caused by regulation, and is the locality of the transition zone between cold and warm reaches likely to stay constant as reregulated flow regimes are implemented?
- Interactions with nonnative fishes may limit recovery of endangered fishes regardless of flow provisions.

The report concludes with recommendations that couple management action (implementation of interim flow regimes) with additional study to resolve the uncertainties presented above. The recommendations reflect an ecosystem approach to resolution of flows needed to protect and enhance the endangered fishes of the Upper Colorado River Basin. In essence, these recommendations constitute a new, holistic instream flow methodology.

- Implement interim flows that reestablish seasonality, with spring peaks that approach the amplitude and frequency of preregulation events, and summer and winter baseflows with daily changes (not daily volume) limited to near preregulation conditions (probably no more than about 5% per day).
- Provide common understanding of water availability so that interim flows can be provided in relation to precipitation and legal flow abstraction in each subbasin.
- Improve the standardized monitoring program as a mechanism to evaluate effectiveness of interim flows by adding a community ecology perspective.
- Diversify the research program to resolve critical uncertainties associated with interim flows.
- Implement a peer review process to ensure that research and monitoring objectives are based on solid science and are responsive to the need to resolve uncertainties associated with the interim flows.
- Implement a management process that can adaptively change the interim flows as new implications from monitoring and research are forthcoming.

The recommended methodology needs unambiguous endorsement to be successful. Success or failure will be judged by long-term trends in the populations of the endangered fishes.

Introduction

Endangered Fishes of the Upper Colorado River Basin

Four endemic fishes, Colorado squawfish (*Ptychocheilus lucius*), bonytail chub (*Gila elegans*), humpback chub (*Gila cypha*), and razorback sucker (*Xyrauchen texanus*), of the Colorado River are protected under the Federal Endangered Species Act, and a recovery program for these fishes has been established by the U.S. Fish and Wildlife Service (Wydoski and Hamill 1991). These endemic, big-river fishes were abundant throughout the potamon[1] reaches of the Upper Colorado River Basin (Fig. 1) during settlement and initial development of the basin (circa 1870's–1950's; Minckley 1973; Quartarone 1993). However, current population size and recruitment of these fishes are reduced substantially, underscoring the rationale for their listing under the Endangered Species Act. Bonytail chub and razorback sucker are virtually extirpated in the Upper Colorado River Basin. Reproducing populations of humpback chub are known only in five canyon segments (Colorado River: Black Rocks and Westwater canyons; Green River: Gray and Desolation canyons; Yampa River: Yampa Canyon). Squawfish remain comparatively abundant, but their distribution is restricted by dams and diversions (Fig. 1). The decline of these fishes is attributed primarily to habitat loss and other environmental changes associated with construction of reservoirs and reduced and regulated flows in the remaining potamon reaches of the fragmented river system (Stanford and Ward 1986a). Predation by numerous introduced species (Minckley et al. 1991; Tyus 1991a, 1991b) and toxic effects of selenium from irrigation return flows (Stephens et al. 1992) also have produced documented pressures on the survival of these fishes.

The recovery program emphasizes reregulation of flows and obtaining water rights to ensure long-term stability of flows so that documented environmental needs of the fish can be met over the long term (U.S. Fish and Wildlife Service 1987a, 1993). Flow regimes have been formally recommended for the Green River (U.S. Fish and Wildlife Service 1992), Yampa River (U.S. Fish and Wildlife Service 1990), and the "15-mile reach" of the mainstem Colorado River in the Grand Valley near Grand Junction, Colorado (Kaeding and Osmundson 1989; Osmundson and Kaeding 1991). However, provision of instream flows is contentious, owing to the high value of water development entitlements apportioned to Colorado, Utah, and Wyoming per the Colorado River Compact. Indeed, the recovery program is predicated on development of these entitlements. Contention also has arisen with regard to the efficacy of technical or scientific methods used to justify flow recommendations.

Purpose and Objectives of the Study

Owing to contention over flow recommendations developed by the U.S. Fish and Wildlife Service, I was commissioned by the Instream Flow Subcommittee of the Recovery Implementation Program for Endangered Fish Species of the Upper Colorado River Basin to review and synthesize the science pertinent to the issue.

The objectives of the study were as follows:

(1) to complete a comprehensive review of past and ongoing technical activities, methods, and knowledge related to the quantification of instream flows needed for recovery of the four endangered fish species in the Colorado and Green River subbasins, including the flow recommendations of the U.S. Fish and Wildlife Service;

(2) to identify critical uncertainties or key issues, technical and nontechnical, related to provision of instream flows; and

(3) to provide recommendations to resolve the technical issues related to quantifying the instream flow needs of the endangered fishes. These objectives could not be met without a thorough reading of the literature describing the biogeochemistry of the river system; thus, I also offer perspective on the quality and completeness of the ecological information base in the context of flow provisions to protect and enhance the fish populations of concern.

Results of this study will assist the Recovery Program members in their decision-making process for meeting the needs of fish and directing future instream flow studies for the benefit of the endangered fishes. Moreover, the report also is intended to be a scientific synthesis of what is known about the ecosystem encompassed by the Upper Colorado River Basin, which has been extensively altered by dams and diversions (Fig. 1).

[1] The downstream zone of a river continuum characterized by warm, often turbid waters, sandy, unstable bottoms, and complex channels that may be constrained in canyon segments but more often meander through broad valley or coastal floodplains (after Illies and Botosaneanu 1963 and Stanford and Ward 1993).

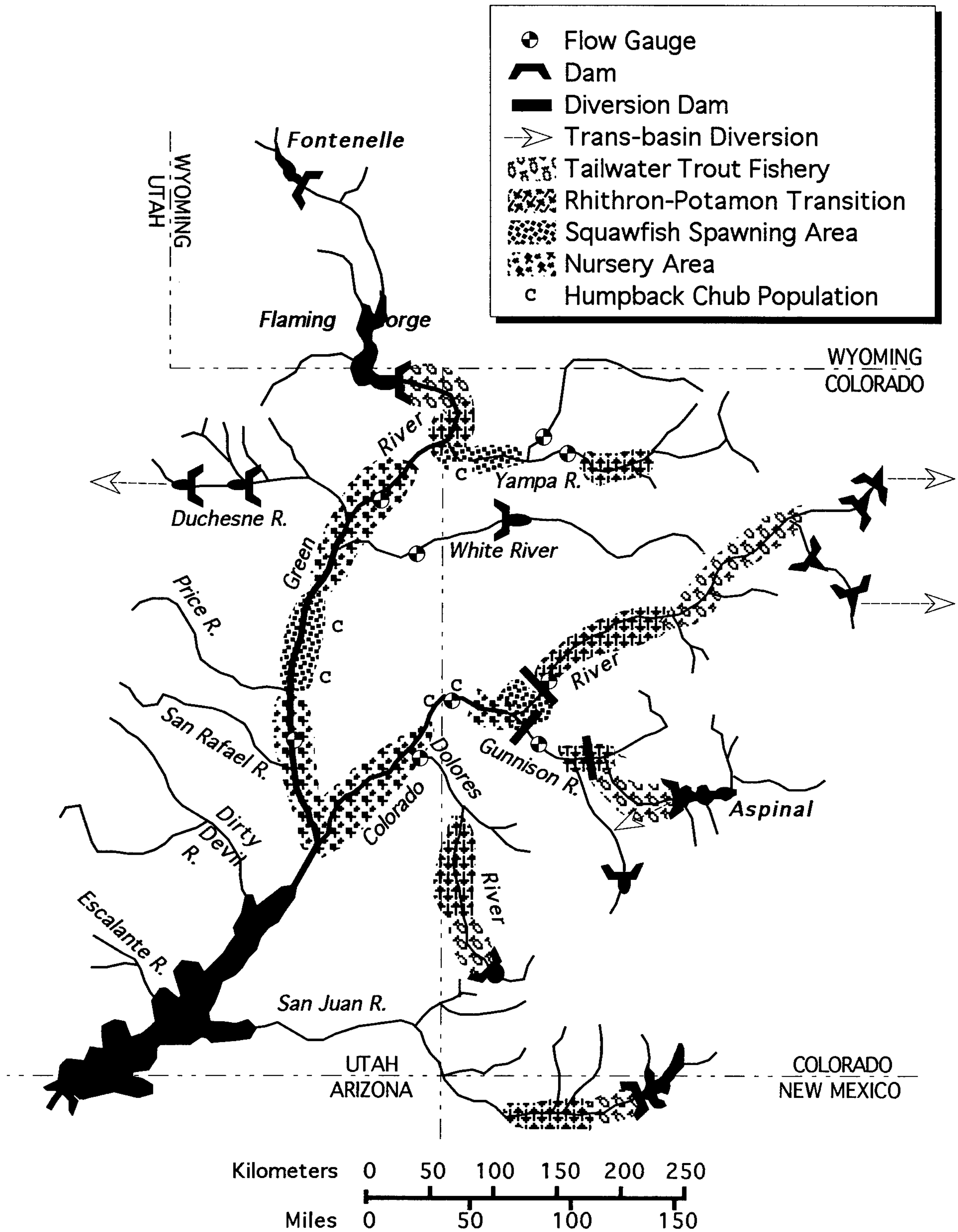

Fig. 1. The Upper Colorado River Basin ecosystem upstream from Lake Powell showing rhithron-potamon transition zones on the largest tributaries, generalized localities of humpback chub populations, localities of squawfish spawning and nursery areas (i.e., alluvial reaches and associated backwaters and wetlands where young-of-the-year and juvenile razorback sucker and Colorado River squawfish are most often found), large hydroelectric or storage dams and diversion dams that regulate discharge and block squawfish and razorback migration, and localities of economically important tailwater trout fisheries (modified from Stanford and Ward 1984, 1986b; Tyus and Karp 1991).

Methods and Approach

Review of Information

I located and read peer-reviewed publications and unpublished reports pertaining to the ecology of the fishes, along with documents providing rationale and data for flow provisions recommended by the U.S. Fish and Wildlife Service. Also, I discussed data, rationale, and issues related to flow provisions with researchers, management personnel, and persons with detailed knowledge of issues pertaining to provision of instream flows. Literature cited in this report includes works that I determined to be most pertinent to an informed discussion of instream flow provisions in the context of the Upper Colorado River Basin and its rare, endemic fishes.

My analysis was limited to review of documents and discussions of data with researchers. Therefore, judgments and conclusions depend on the quality and quantity of data presented in the documents or provided to me in unpublished form. However, I noted from the outset that many of the key observations about these fishes and the rivers in which they live have been published in peer-reviewed literature. Indeed, the occurrence of peer-reviewed papers is high in relation to the dollars invested in research on these fishes compared with other multimillion dollar programs I have reviewed (i.e., Glen Canyon EIS; Columbia River Fish and Wildlife Program). Reviewed publication does not guarantee accuracy of data or interpretations, but it is the best standard of credibility we have in science.

Peer Review and Schedule

During the study period, which began in October 1992, I reported monthly to the Instream Flow Subcommittee to facilitate communication and understanding of the objectives of the study, my approach, and understanding of issues. Assembly and review of literature and dialog with persons working on the problem were completed in May 1993.

I was assisted in preparing this report by advice and comment from an expert panel consisting of Edmund D. Andrews (U.S. Geological Survey, Boulder, Colorado), William J. Matthews (University of Oklahoma Biological Station, Kingston), and James V. Ward (Colorado State University, Fort Collins). I met with the expert panel 18–19 April 1993 in Grand Junction, Colorado. I provided the panel with a preliminary version of this report, and we viewed sites on the Colorado and Gunnison rivers from aircraft, visited sites in the 15-mile reach with Doug Osmundson (U.S. Fish and Wildlife Service, Grand Junction, Colorado), and discussed my review and preliminary conclusions. Written reviews of first and second drafts of this report were provided by the expert panel and members of the Instream Flow Subcommittee. Many other scientists and experts working in the Upper Colorado River Basin also provided written comments on the second draft. All the comments I received were insightful, and I attempted to address all concerns that I felt would improve the report. I was especially cognizant of comments by the expert panel, and the panel's input is evident throughout the document. However, I take full responsibility for the accuracy and completeness of information and conclusions in the report.

Ecological Context for Instream Flow Analysis

I approached this analysis from an ecosystem perspective, recognizing that ecological processes or management actions in one subbasin or river reach may influence processes in others (i.e., system components are ecologically interconnected). For example, migrations by fishes ecologically interconnect the entire river system, except as influenced by dams, which usually block upstream movements. Dams and reservoirs rarely prevent fishes from moving downstream, although mortality may be high in passage, and conditions downstream from the dams may or may not favor colonization by fishes living upstream from the impoundment. My point is that reaches in the river system where the endangered fishes live (i.e., downstream from the larger dams) are hydrologically and ecologically connected to upstream reaches, where the endangered fishes may have never existed. Interactions between flow dynamics and channel and floodplain features vital to the existence of the endangered fishes also occur from river reach to catchment scales and represent another example of ecosystem connectivity. Hence, the ecosystem in this analysis included the entire Upper Colorado River Basin (Fig. 1).

Uncertainty exists as to whether ecological and water regulation processes in Lake Powell have significant influences on the ecology of the Upper Colorado River Basin. Regulation of Lake Powell is influenced by delivery of water from the Upper Colorado River Basin, and the reservoir is a source

of nonnative fishes that may migrate upstream, thereby influencing the native fishes living in the Upper Colorado River Basin. However, I viewed Lake Powell as the downstream boundary of the river ecosystem examined in this report (Fig. 1).

A vital characteristic of river ecosystems is that their biophysical processes are inherently variable. The essence of ecology is understanding the complex processes that control observed variability in the distribution and abundance of biota. Quantification of the structure and function of complex systems, like the Upper Colorado River Basin ecosystem, in time and space must be based on long-term (> 5 years) measurements to detect patterns or trends that in shorter time frames are overwhelmed by variability. Hence, an ecosystem approach strives to determine how and why the river changes in time and space, not simply to describe current conditions.

Like most scientists, I view model building and logistic descriptions of dynamic events in ecology as mechanistic tools for formalizing a better understanding of what is known about a system; such tools should not be used to predict the future. Predicting the consequences of environmental change is the ultimate challenge of contemporary ecology. This must be resolved through strong inferences based on properly scaled measurements of biophysical variables that integrate the myriad system-specific ecological processes that are spatially and temporally dynamic (Magnuson 1990; Stanford and Ward 1992a). The problem of instream flow provision must be resolved from strong inferences derived from long-term trends in ecological processes and responses of the river ecosystem in which the endangered fishes live.

River Ecology and Effects of Regulation on the Endangered Fishes of the Upper Colorado River Basin

Ecology of the Endangered Fishes

Information about the endangered fishes is very detailed, given that they are relatively rare fishes; several reviews of the scientific information have been published (e.g., Stanford and Ward 1986b; Minckley et al. 1991; Tyus 1991a). Therefore, I repeat here only salient points of particular importance to my review of the flow recommendations made by the U.S. Fish and Wildlife Service.

As noted above, the historical range of the four species included the potamon and transitional reaches of the Green and Colorado river systems, including most of the larger tributaries, in particular the Yampa, White, Dolores, and Gunnison rivers. Today, ranges of these fish are fragmented by dams and diversions, and populations have declined significantly in relation to distributions at the turn of the century (Quartarone 1993). Bonytail chub are close to extirpation, but they have been successfully cultured, along with humpback chub, squawfish, and razorback sucker, at the Dexter National Fish Hatchery, Dexter, New Mexico (Johnson and Jensen 1991), and brood stocks currently are being held in several locations. Because of their comparative rarity in the wild, ecological information on the historical range of bonytail chub is more fragmentary than for the other species. A few specimens of bonytail chub were collected in the 1970's in the Green and Yampa rivers (Kaeding et al. 1986), but their phenology (life history) and exact cause of disappearance in the Upper Colorado River Basin system are unknown.

Humpback chub are found only in whitewater canyon segments (Fig.1). Migrations are limited, and humpback chub may have always been restricted to specific canyon segments, at least as adults. Spawning in the Upper Colorado River Basin occurs on the declining limb of the spring runoff event in association with the 20° C isotherm (Kaeding and Zimmerman 1983). Humpback chub interact behaviorally (and probably hybridize) with congeneric, endemic roundtail chub (*Gila robusta*), which are more abundant throughout the Upper Colorado River Basin (Kaeding et al. 1990; Karp and Tyus 1990). Much of what is known about the life cycle of humpback chub is based on unpublished studies in the Grand Canyon, where they migrate from the regulated Colorado River into the unregulated Little Colorado River to spawn. Similar migratory behavior has not been documented in the Upper Colorado River Basin, and exact locations of spawning sites are unknown (Richard Valdez, BioWest Inc., Logan, Utah, personal communication; Larry Crist, U.S. Bureau of Reclamation, Salt Lake City, Utah, personal communication).

Lanigan and Tyus (1989) estimated that only 978 ± 232 adult razorback sucker remained in the Green River above Desolation Canyon during 1981–86, which very likely is only a small fraction of the historic population. Some researchers believe that significant declines have occurred since

1970. However, accurate annual population estimates, based on recovery of fish tagged in the earlier study, are biased by differential tag retention, although the population clearly has remained "much less than 1,000" (Kenneth P. Burnham, Colorado State University, 1 June 1993 letter to Tim Modde, U.S. Fish and Wildlife Service, Vernal, Utah). A few young razorback sucker have been collected in the Green River in recent years (e.g., three fish <415 mm in 1993; Tim Modde, personal communication), and the age structure of the few razorback sucker collected annually on the Colorado River has declined in recent years (Chuck McAda, U.S. Fish and Wildlife Service, Grand Junction, Colorado, personal communication). Thus, some recruitment of adult cohorts may be occurring in the Green and Colorado rivers, perhaps related to higher flows. Whether stable or declining, the population of razorback sucker in the Green–Yampa system probably has not exceeded more than 1,000 fish in the last 2 decades. Because most of the very few razorback sucker captured in the Upper Colorado River Basin are older fish, I conclude, as did Tyus (1991a), that very little recruitment of adult razorback sucker has occurred since the 1960's.

Razorback sucker have been observed spawning or in spawning condition (ripe) during the rising limb of the spring runoff at temperatures 5–10° C below (McAda and Wydoski 1980; Tyus 1987) the experimentally observed optimum range (20–22° C) for reproduction (Inslee 1982; Hamman 1985; Marsh 1985). Razorback sucker were commonly (50 or more per year) collected in the 15-mile reach of the Colorado River in the early 1970's, mostly in a gravel pit connected to the river near Grand Junction, Colorado (McAda and Wydoski 1980; Valdez and Wick 1983). That gravel pit washed out in the 1984 spring flood of record, and only incidental captures were made subsequently (Osmundson and Kaeding 1991). However, in spring 1993, 67 razorback sucker were taken from another gravel pit (Etter Pond). One 20-year-old fish was collected, but the rest were 9 years old, corresponding to spawn during the 1984 flood, when the pond was last connected to the river (Chuck McAda, personal communication).

In addition to their propensity to inhabit manmade gravel pits that are at least ephemerally connected to the river, razorback sucker are most often captured in low velocity habitats in the channel (Fig. 2) and wetland ponds connected to the channel (McAda and Wydoski 1980; Tyus et al. 1987). Bulkley and Pimentel (1983) showed that razorback sucker preferred temperatures of 22–25° C in shuttle box experiments. In the potamon reaches of the Upper Colorado River Basin, shallow, backwater, and wetland habitats are typically closer to the preferred temperatures than is the river channel, especially in the upstream reaches, where razorback sucker are most commonly found. Indeed, Wick et al. (1983) showed that backwaters flooded by spring runoff on the Yampa River were significantly warmer than the channel, thereby offering more degree-days for maturation of spawning condition. Naturally functioning backwaters (i.e., not influenced by erratic, regulated flows) also contain food sources, such as zooplankton, invertebrates associated with macrophytes, and microbially rich detritus, needed to mediate growth of razorback sucker (Wick et al. 1982; Wick 1991).

The reproductive bottleneck that is preventing recruitment of razorback sucker in the Upper Colorado River Basin is unknown. Clearly, these suckers prefer lacustrine-like environments, owing to their proclivity for low velocity habitats, especially flooded gravel pits and wetlands, during high flows. River flow regulation, wetland revetments, diversion dams (which limit migratory pathways; see Fig. 1), and presence of abundant native and nonnative predators (also discussed below with regard to similar influences on squawfish) may prohibit the fish from using backwaters and seasonally flooded wetlands in a manner that will allow recruitment to occur annually. Indeed, in Lake Mohave on the Lower Colorado River, where a large population of razorback sucker has persisted for many years but did not recruit in spite of apparent spawning success each year, the recruitment bottleneck was attributed to predation of larvae and early juveniles by nonnative minnows and sunfish (Marsh and Langhorst 1988; Marsh and Minckley 1989; Papoulias and Minckley 1992). The recruitment bottleneck for razorback sucker in the Upper Colorado River Basin very likely relates to the current paucity of low velocity, warm, food-rich, and nonpredator-dominated habitats during spring and summer.

Instream flow recommendations are based predominantly on ecological knowledge of Colorado River squawfish, which are the most abundant and best known of the endangered big river endemics. Squawfish occur most abundantly in the potamon reaches of the Yampa, Green, White,

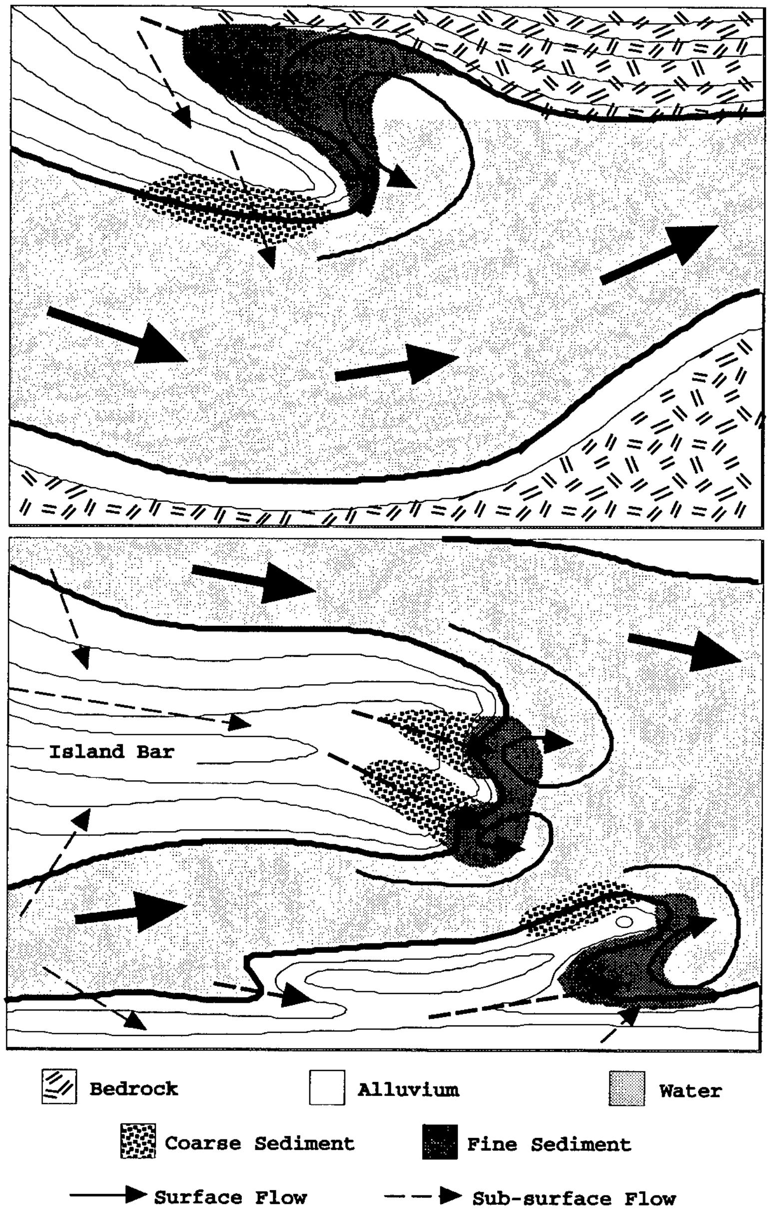

Fig. 2. Schematic representation of geomorphic processes that form low velocity habitats in constrained (canyon, *top panel*) and unconstrained alluvial (floodplain, *bottom panel*) reaches of the Upper Colorado River Basin where endangered fishes are routinely found. In both panels the current condition is baseflow. In the top panel a wall-based channel formed during a higher flow period, creating an eddy that persists and causes deposition of fine sediment in the backwater at the downstream end of the channel. Declining flows from the preceding high discharge period also increased the velocity of water draining across the point bar, thereby leaving clean, coarse cobble. In the bottom panel a midchannel or island bar and a back-bar channel were built during high flow, allowing low velocity habitats to form on the downstream ends. Chute channels of clean cobble formed on the steep, downstream edge of the island bar, as velocity increased with declining volume of flow over the bar. At baseflows, fine sediments are deposited on the aggraded portion of the bar front in relation to river stage. The back-bar channel and point bar function similarly to the wall-based channel. In all cases river water penetrates the alluvium at the upstream end of the bar creating interstitial, subsurface flow that discharges into the low velocity environments and the river as change in elevations reverses the piezometric (downward) gradient to the water table. Hence, habitats used by endangered fishes are dynamic in time and space and are controlled by sediment supply and size, channel morphometry (especially slope and relative constraint by bedrock), and the volume and duration of the previous peak flow events (developed from Tyus 1984, Harvey et al. 1993, and discussions with Jack Schmidt, Utah State University, Logan).

Gunnison (i.e., downstream from the Redlands diversion dam; a few are isolated upstream), and mainstem Colorado rivers (downstream from the Grand Valley diversion dams; Fig. 1).

Colorado squawfish are long-lived piscivores that grow to more than a meter in length and exhibit long migrations (e.g., between White and Yampa rivers; Tyus 1990) associated with 15–20° C isotherms (my interpretation based on data in Tyus 1984, 1990). The fish spawn on chute channels (Harvey et al. in press) that form on specific alluvial bars in the Yampa and Green rivers (Fig. 2) in association with the decline of spring runoff and spates (Nesler et al. 1988; Tyus 1990). Eggs of squawfish hatch within about 5 days after spawning at 20–22° C, which is the critical temperature for successful reproduction (Hamman 1981; Haynes et al. 1984; Tyus and McAda 1984; Marsh 1985). Upon hatching, larvae drift downstream (Fig. 3), where they are entrained in backwater nursery habitats in alluvial reaches (shown generally in Fig. 1). In lab experiments, young of the year (YOY) prefer and grow best at 25° C (Black and Bulkley 1985). The YOY and juveniles are most often found in specific low velocity environments, created by the complex relationship of flow and channel geomorphology (Fig. 2). These nursery and rearing sites also are inhabited by native and nonnative fishes, particularly flannelmouth sucker (*Catostomus latipinnis*), roundtail chub, green sunfish (*Lepomis cyanellus*), red shiner (*Cyprinella lutrensis*), sand shiner (*Notropis stramineus*), and channel catfish (*Ictalurus punctatus*), that compete with the endangered fishes for available food resources or prey on them directly (Valdez and Wick 1983; Karp and Tyus 1990). Adult squawfish also prefer areas of the channel that are braided and complex, where low velocity habitats (e.g., eddies, pools, and slow runs) are abundant. Like razorback sucker, adult squawfish tend to move in and out of large backwaters that form on downstream ends of backbar channels and terrace- or wall-based channels (Fig. 2), which remain connected to the main

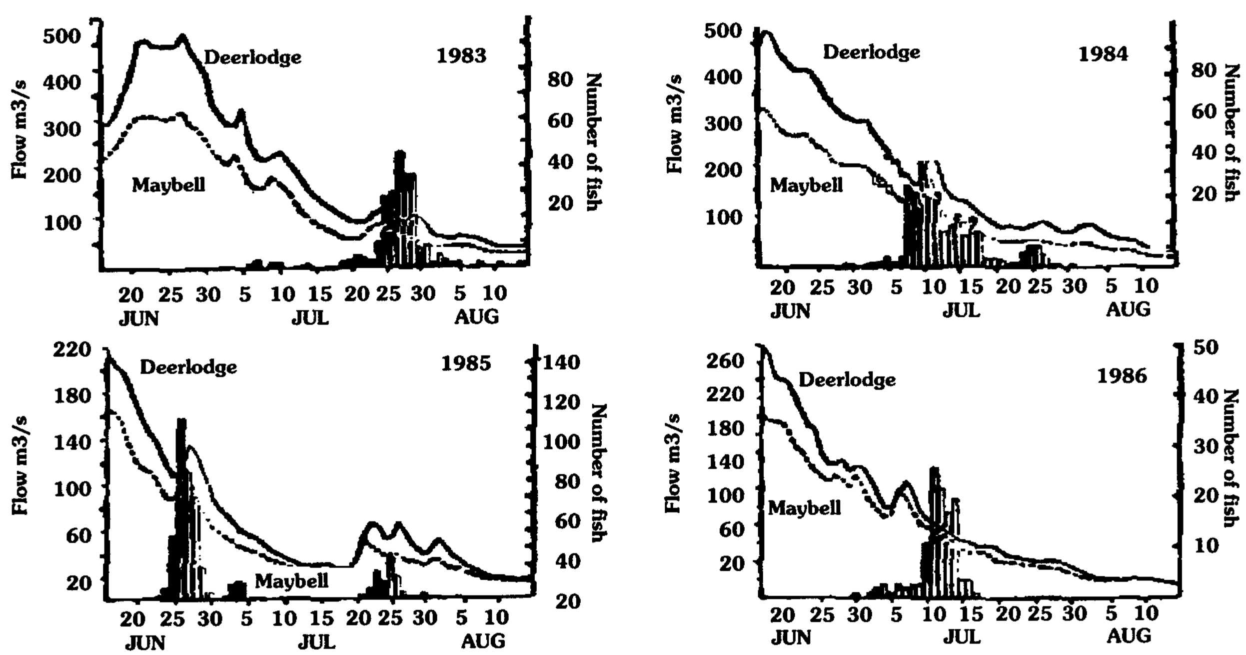

Fig. 3. Relationships of Colorado River squawfish spawning dates (*vertical bars*, data derived from larval drift rates adjusted for hatching time) to Yampa River flows measured at the Deerlodge and Maybell gauges in 4 years. Number of fish represents number of larval fish sampled and distributed according to estimated spawning date (from Nesler et al. 1988).

channel at baseflows. They may feed in these environments (Valdez and Wick 1983) or simply move into low velocity habitats to avoid the higher flow of the main channel (Doug Osmundson, U.S. Fish and Wildlife Service, Grand Junction, Colorado, personal communication). Growth is optimum at 25° C, based on experimental studies; Kaeding and Osmundson (1988) showed that growth in the 15-mile reach of the Colorado River was reduced because maximum temperatures were less than optimum for maximum growth year round. Warmer temperatures in backwater environments could offset the coldwater effect (Wick et al. 1983), assuming food supply is adequate and small squawfish can avoid predation.

Long-term monitoring data strongly indicate to researchers in the recovery program that numbers of larval and YOY squawfish and subsequent year classes are highest when intermediate (about the long-term average) peak flows occur during spring runoff. Numbers of YOY were substantially lower on years of very high spring flows (e.g., flow peaks of record in 1983 and 1984 at the state line gauge, Fig. 4; Osmundson and Kaeding 1991), owing either to poor spawning conditions or mortality associated with flushing effects of high runoff. However, Tyus and Haines (1991) observed higher recruitment of YOY on low flow years in the Green River. Low recruitment of YOY on low flow years in the Colorado River may be related to lack of suitable habitat, either for spawning or rearing or both. An alternate interpretation of Fig. 4 is that the extremely high flows of 1983–84 created or rejuvenated substantial spawning habitat that was available but gradually deteriorating during 1985–88. Regardless of how the relationship is interpreted with respect to the peak (1983–84) and low (1982) flow events, production of young squawfish can occur over a very wide range of spring flows (i.e., the recruitment threshold of YOY is very wide). Like McAda and Kaeding (1991). I conclude that squawfish spawning may be much less site-specific than is suggested by the literature, or a very wide range of preferred spawning conditions exists on the spawning bars where squawfish are routinely found (e.g., Cleopatra's Couch Bar on the Yampa; Three Fords on the Green).

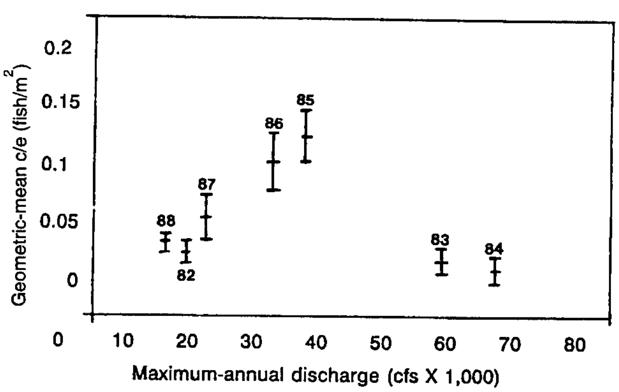

Fig. 4. Catch per effort of postlarval squawfish as related to maximum annual discharge for the Colorado River. Data are geometric means ±1 standard error for fish collected in backwaters using standardized sampling protocol (U.S. Fish and Wildlife Service 1987b) during October between the Westwater Canyon (km 177) and confluence with the Green River (km 0). Thus, these data are a relative measure of recruitment from spawning that occurred during the high flow periods each year (from McAda and Kaeding 1989, also included in Osmundson and Kaeding 1991). Data collected in 1989–1991, which were low to average water years, are consistent with this relationship (C. McAda, U.S. Fish and Wildlife Service, Grand Junction, Colorado, unpublished data).

The life history strategy of squawfish seems to be strongly influenced by the propensity of the larvae and juveniles to drift far downstream from the spawning site; survivors subsequently move back upstream as they mature. Adults, especially large fish (Fig. 5), are most commonly found at or near the potamon-rhithron[2] transition zone in the Yampa and Colorado rivers. Recruitment of adults presumably is lower for cohorts spawned in low-flow years, owing to reduced spawning success to start with and increased predation pressure per fish during each subsequent life history stage. Predation on YOY and juveniles may be more intense in low-flow years, when habitats are confined. The positive relation between year-class strength and peak discharge generally seems to hold for the Green and Colorado rivers (Tyus and Karp 1989, 1991; Osmundson and Kaeding 1991) and also applies to humpback chub in the Grand Canyon (R. Valdez, personal communication). Recruitment seems weak in very high- and low-flow years and relatively good in years of long-term average flows.

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[2] Headwater reaches of a river continuum characterized by cold, clear water, bedded gravel and cobble substrata on the river bottom, and alternating canyons (constrained) and intermontane floodplains (less constrained).

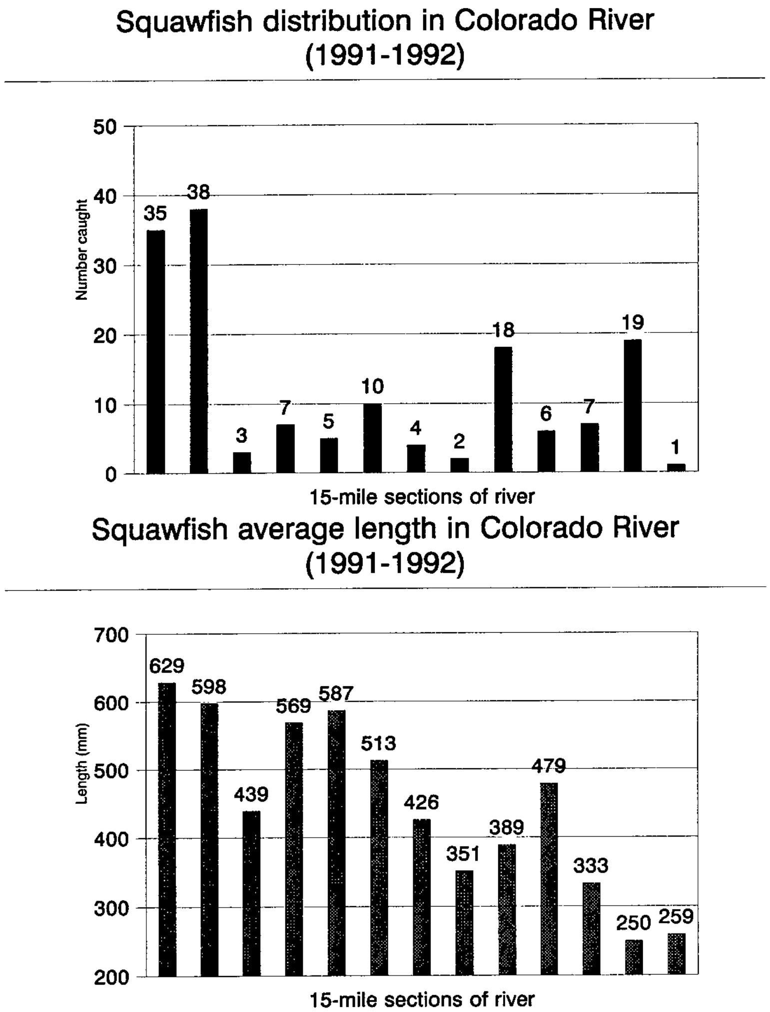

Fig. 5. Distribution of squawfish by size and number caught in the Colorado River from the Green River confluence (km 0) to the Grand Valley diversion dam at the top of the 15-mile reach during 1991–1992. This relationship, although variable, is remarkably consistent from year to year; the upstream areas inhabited by by larger adults are consistently devoid of young-of-the-year squawfish relative to the river segment below Westwater Canyon and the confluence with the Green River (km 179–0) (Doug Osmundson, U.S. Fish and Wildlife Service, Grand Junction, Colorado, unpublished data).

Dynamic Relationships Between Flow, Channel Geomorphology, and Food Webs

Distribution, abundance, and life histories of the endangered fishes seem to be strongly influenced by availability of physical habitats that are created and maintained by flow dynamics in time and space (Fig. 6). Indeed, squawfish only spawn on clean cobble on specific bars in the sediment-laden river segments of the Upper Colorado system. Hence, a fundamental process-response relationship involves the movement of the fish to the bars in concert with flows that first form the bars and then flush sediment off of cobble substratum so that the fish can spawn successfully (Fig. 2; Tyus 1990; Harvey et al. in press). Humpback chub primarily occur in eddies and other hydraulically complex habitats found in constrained channels in the steeper gradient segments within canyons (Fig. 2; Kaeding and Zimmerman 1983; Kaeding et al. 1990; Karp and Tyus 1990; Valdez et al. 1990). Squawfish and razorback sucker are almost always captured in low or zero velocity habitats (Tyus 1984; Osmundson and Kaeding 1989), which occur within the active channel (e.g., eddies) or exist as backwaters (e.g., back-bar channels) or floodplain wetlands (i.e., flooded bottomlands) that are continually or seasonally attached to the active channel. Squawfish (Tyus 1991a, 1991b), and perhaps razorback sucker (Minckley et al. 1991), must have access to low velocity environments to mature. These observations strongly imply that low velocity habitats are important feeding or resting areas or both, but they do not imply that rivers of consistently low velocity or volume are most suited to the endangered fishes of the Upper Colorado River Basin.

Low velocity environments are formed and maintained by complex hydrologic processes that

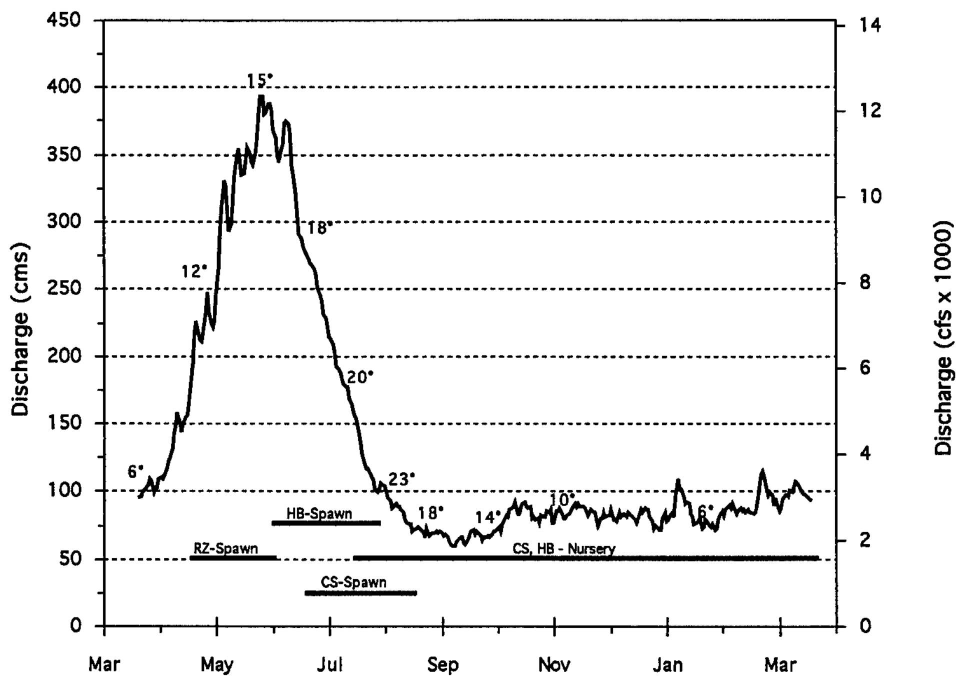

Fig. 6. Generalized relationship between average daily flows in the Green River (Jensen gauge:1980–91), river temperatures (° C), and the timing of life history events of squawfish (CS), humpback chub (HC), and razorback sucker (RZ) (modified from Tyus 1990, Tyus and Karp 1991, flow data from U.S. Geological Survey).

involve the frequency and duration of high velocity, peak flows and associated flux of sediment through the stream segment (cf., Andrews and Nelson 1989). Hence, occurrence of low velocity habitats is dynamic in space and time and strongly linked to the flow regime, sediment supply, and channel morphology. Numbers and area of low velocity environments used by squawfish larvae, juveniles, and sometimes adults in the alluvial Jensen and Ouray areas of the Green River (Tyus and Haines 1991) apparently are maximized at a given time at river discharge of 1,381 cfs (numbers) or 1,687 cfs (area; Pucherelli et al. 1990). However, a river stage-backwater relationship observed in a particular year is determined by the volume and duration of the peak flow events that occurred during spring runoff or other intense spates in that year or in the year or two immediately preceding the measurements. Instream flows designed to provide maximum access for endangered fishes to low velocity habitats must be based on long-term measures of the relation between peak flows and channel and backwater configuration, even in river segments where delivery of sediments is equal to export (quasi-equilibrium systems). This is especially true in alluvial segments that may be aggrading, as in the Escalante Bottom and Ouray areas of the Green River (Andrews 1986), because channel configurations may change significantly in response to variable peak flows. As the channel morphology changes from year to year, a given discharge will vary in its inundation of backwaters and bottomlands, which can profoundly influence fishes and other biota that must move into backwaters, flooded bottomlands, and other low velocity habitats from the channel and back again in short (diel) and long (seasonal) time frames. Therefore, efforts to build process-response models of flow and physical habitat relationships (e.g., Harvey et al. in press) must take into account that flow and substratum relations in most riverine environments are stochastic and cannot accurately be described by linear or logistic functions. Indeed, complex channels that promote occurrence of low velocity habitats are virtually always characterized by nonuniform flows in time and space, whereas many models often assume uniform flow.

Given that a relationship exists between flow dynamics and availability of various physical habitats preferred by the fish, what role do these habitats play in the trophic ecology of the river? Except during periods of high turbidity, the rivers in the

Upper Colorado River Basin, in general, are intensely autotrophic and capable of supporting very productive benthic food webs on cobble substratum of riffles in the steeper segments (Annear 1980; Annear and Neuhold 1983; Carter and Lamarra 1983; Ward and Stanford 1991). Although not conclusively documented in the Upper Colorado River Basin, backwater environments, which are most abundant in the alluvial segments, are apparently very productive after spring runoff owing to the flux of clear, nutrient-rich water through them from hyporheic sources (Fig. 2) and warmer temperatures than occur in the channel, both of which are associated with the approach of baseflows in summer. However, channel areas in alluvial segments are probably not as productive owing to the unstable nature of the sand and mud bottoms (Ward et al. 1986; Ward and Stanford 1991). Moreover, as one moves downstream toward Lake Powell on either the Colorado River or the Green River, recruitment of fine sediments increases. The lower reaches of both rivers are characterized by extensive deposits of silt and clay (E. D. Andrews, U.S. Geological Survey, Boulder, Colorado, personal communication), which may limit zoobenthos production. Indeed, zoobenthos species richness and biomass decline downstream from the rhithron-potamon transition zone as the river bottom changes from coarse to fine substratum (Carter and Lamarra 1983; Ward and Stanford 1991).

These studies and discussions with researchers indicate that food webs are more stable, complex, and productive in the upstream reaches of the potamon, associated with cobble substratum within the channel (e.g., Yampa Canyon, 15-mile reach, lower Gunnison River). In the alluvial segments of downstream reaches on the Green and Colorado rivers, productive food webs may only be present in low velocity backwaters and the few cobble bars. Studies have been inconclusive as to exactly how productive backwater environments actually may be, but algae, zooplankton, and mud-dwelling midge (Chironomidae) larvae are present in backwaters on the Green River (Grabowski and Hiebert 1989). I would expect naturally functioning backwaters (i.e., seasonally flooded and continuously connected to the channel) to contain rooted aquatic vegetation (i.e., as opposed to encroaching riparian vegetation), which provides substratum for algae, odonates, snails, mayflies, and caddisflies, in addition to forms living on the bottom (e.g., oligochaetes and midges). Organic detritus originating in the river channel (e.g., periphyton, drifting leaves) also may be deposited in low velocity habitats, providing substratum for detritivorous insects and fishes. Hence, backwater food webs typically have abundant forage for small fish, such as YOY squawfish, which are then available to larger predators. A large body of literature supports the concept that naturally functioning floodplain wetlands of rivers are very productive and an essential component of the life history of fishes that migrate between channel and floodplain wetlands (e.g., Welcomme 1979; Junk et al. 1989; Ward 1989; Petrere 1991).

Because they fringe the channel rather than extend across it, backwaters and associated floodplain wetlands are more ephemeral than cobble bars, which remain partially inundated even at the lowest flows. Moreover, backwater and wetland (flooded bottomland) environments in many unconstrained (floodplain) areas of the Upper Colorado River Basin have been ecologically disconnected from the river channel either by man-made revetments or by sand bars or encroaching riparian vegetation that are no longer scoured owing to truncation of peak flows by regulation (e.g., Graf 1978; Stanford and Ward 1986a). Indeed, I believe loss of productive backwater environments may explain, in part, why humpback chub are found only in canyon segments and why razorback sucker and squawfish move around a great deal. Food webs associated with gravel bars are probably more productive and permanent (e.g., Ward and Stanford 1991), and the larger razorback sucker and squawfish adults must search for these more productive sites because of their large size and need for abundant, large forage items. Squawfish adults may be most commonly found in or near the rhithron-potamon transition zone (Fig. 5) because the transition zone is the only area with sufficient productivity and a permanent food web to support the life history energy balance of this large predatory animal. Indeed, other native fishes that are the natural prey of adult squawfish, especially roundtail chub and bluehead sucker (*Catostomus discobolus*), are more abundant in or near the transition zones (Doug Osmundson, personal communication), where algae and zoobenthos forage probably are most abundant.

The trophically dynamic nature of the potamon reaches of the Upper Colorado River Basin and the interactive influences with geomorphic controls are poorly understood aspects of the ecology of the endangered fishes. On the one hand, these fishes prefer low velocity habitats; on the other hand,

these low velocity habitats may not be as productive as higher velocity reaches because of fluctuating flows caused by regulation. Measurements are needed to more firmly establish cause and effect. The problem is complicated because site-specific velocities vary with flow, which is precisely why channel geomorphology is so complex and dynamic in time and space. I conclude that throughout their life cycles these fishes are highly adapted to variations in flow velocity, depth, turbidity, and food web structure and function associated with this spatially and temporally dynamic biophysical interaction. They simply move around as flow varies, constantly seeking the best energy return on energy invested in foraging. In the case of squawfish, large size apparently provides for considerable movement, which allows them to efficiently use a highly variable environment. Anthropogenic activities, such as revetment of floodplains and erratic regulation of baseflows by dams and diversions, change the natural biophysical variability and reduce the variety of habitats available, thereby compromising the life history energy balance of the fishes (Ward and Stanford 1989).

Influences of Stream Regulation

Flows in the Green and Colorado River subbasins have been depleted by diversions and further regulated by hydroelectric releases from large storage reservoirs (Figs. 1, 7, 8, and 9). Of the larger tributaries, only the Yampa remains essentially free flowing, although regulation of the White River is not severe (i.e., the mainstem dam is a low-head structure, and water depletions are about the same as on the Yampa). To examine the rationale for provision of flows to recover the endangered fishes, one must understand how the river ecosystem has been changed by regulation. The ecological effects of stream regulation have been extensively reviewed and summarized (cf., Ward and Stanford 1979; Lillehammer and Saltveit 1984; Petts 1984; Stanford and Ward 1986b; Craig and Kemper 1987; Carlson and Muth 1989; Gore and Petts 1989). I discuss only salient aspects of the problem here.

Alteration of Flow, Temperature, and Sediment Regimes

Regulation has reduced the spring peaks of the snowmelt-dominated rivers of the Upper Colorado River Basin and increased the baseflows (see figures in Stanford and Ward 1983 and Andrews 1986). Hydroelectric operations also have increased short-term (hourly, daily) flow variability (e.g., Figs. 10–14). Note that extreme hourly variation may be masked by presentation of flow as daily means (compare Figs. 12 and 13 with August and September data in Fig. 14). Daily means are usually plotted in analyses of flow durations because hourly data are reduced to daily means in the long-term data bases for stream flows maintained by the U.S. Geological Survey.

Rivers regulated by hypolimnial (bottom) release dams (e.g., Aspinall Units on the Gunnison) are cooler in summer and warmer in winter for many miles downstream from the dam than before impoundment (Stanford and Ward 1983), although Flaming Gorge Dam was retrofitted with a selective withdrawal system to ameliorate negative effects of cold temperatures on fish growth downstream from the dam (Stanford and Ward 1986a).

Retention of sediments within impoundments such as Flaming Gorge and the Aspinall Units has reduced suspended sediment concentrations and bedloads downstream from the dams. Moreover, loss of peak flows has reduced the transport power of the river. Therefore, sediment discharges from tributaries downstream from the point of regulation are more persistent; alluvium and colluvium entering the river channel are not moved downstream with predam efficiency (personal observation in the Upper Colorado River Basin and documented in the Grand Canyon by Dolan 1978 and others). Thus, riverine sediment budgets and channel elevations may change significantly after regulation. In the Green River, mean annual sediment discharge decreased by 54% at Jensen and 48% at Green River, 169 and 467 river kilometers downstream from Flaming Gorge Reservoir (Andrews 1986). A new quasi-equilibrium between sediment supply and transport has been attained in the Green River (Lyons and Pucherelli 1992), resulting in a decrease in the bankfull channel of 6% (Andrews 1986) to 10% (Lyons and Pucherelli 1992). Loss of channel area is attributed to formation of new islands and increased island size and loss of side channels that filled with bed materials (Lyons and Pucherelli 1992). In the Gunnison Gorge of the Gunnison River downstream from the Aspinall Units, summer thunderstorms in 1991–92 caused debris flows in normally dry side-flow channels. This episodic inflow of rocks and soil created large alluvial fans out into the river, which have persisted owing to insufficient peak

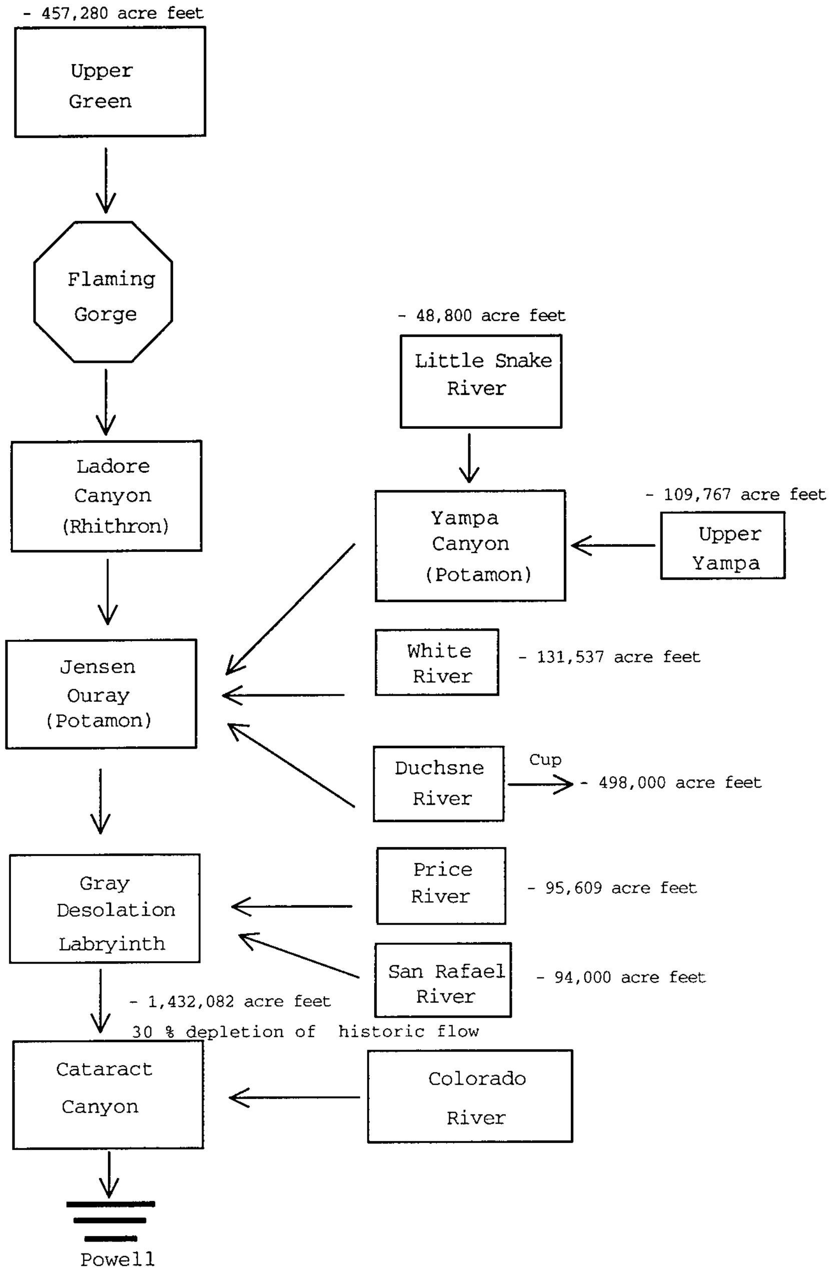

Fig. 7. Regulation of flow in the Green River system. *Octagons* represent storage reservoirs, *reversed arrows* indicate transcatchment diversions, and annual flow depletions are given in acre-feet.

flows to flush alluvium downstream (Elliott and Parker 1992).

Channel Encroachment by Riparian Plants

The inability of the regulated river to redistribute alluvium allows encroachment of vegetation into the river channel. Dense vegetation down to the low water mark (i.e., minimum flow channel) is an ecological feature that now characterizes the river corridor of the regulated segments of the Gunnison (Stanford and Ward 1984), Colorado (Graf 1978; Stanford and Ward 1986b; Osmundson and Kaeding 1991), and Green rivers (Fisher et al. 1983). However, Fisher et al. (1983) also provided very clear evidence that vegetation along the shoreline of the Yampa River has not changed

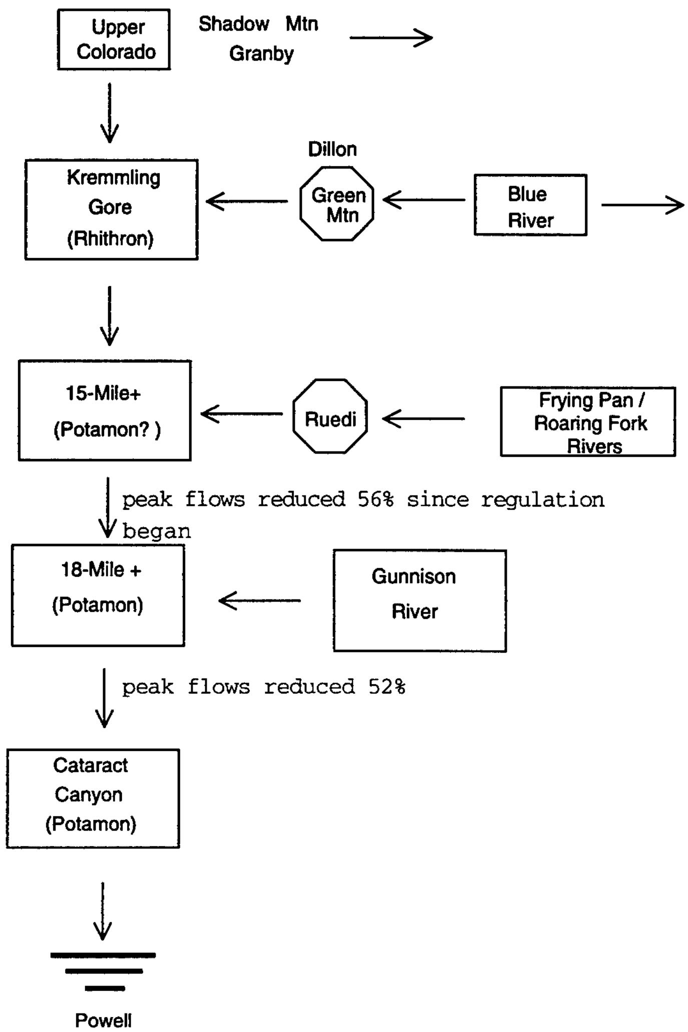

Fig. 8. Regulation of flow in the Colorado River system, upstream of the confluence with the Green River. *Octagons* represent storage reservoirs, and *reversed arrows* indicate transcatchment diversions.

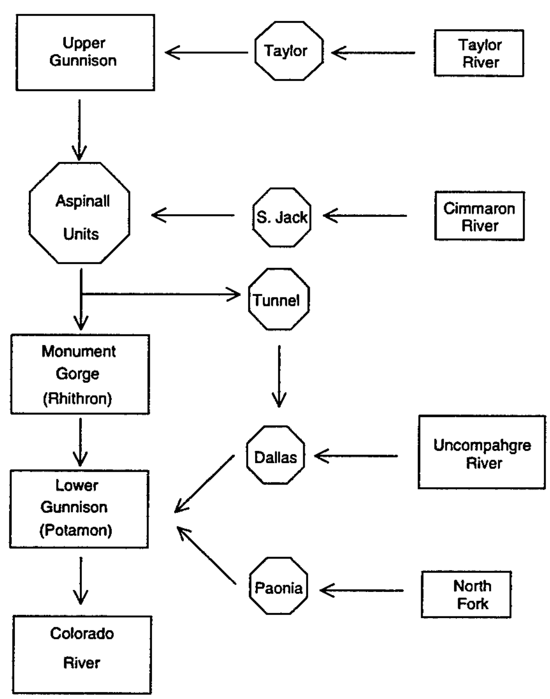

Fig. 9. Regulation of flow in the Gunnison River system. *Octagons* represent storage reservoirs, and *reversed arrows* indicate transcatchment diversions.

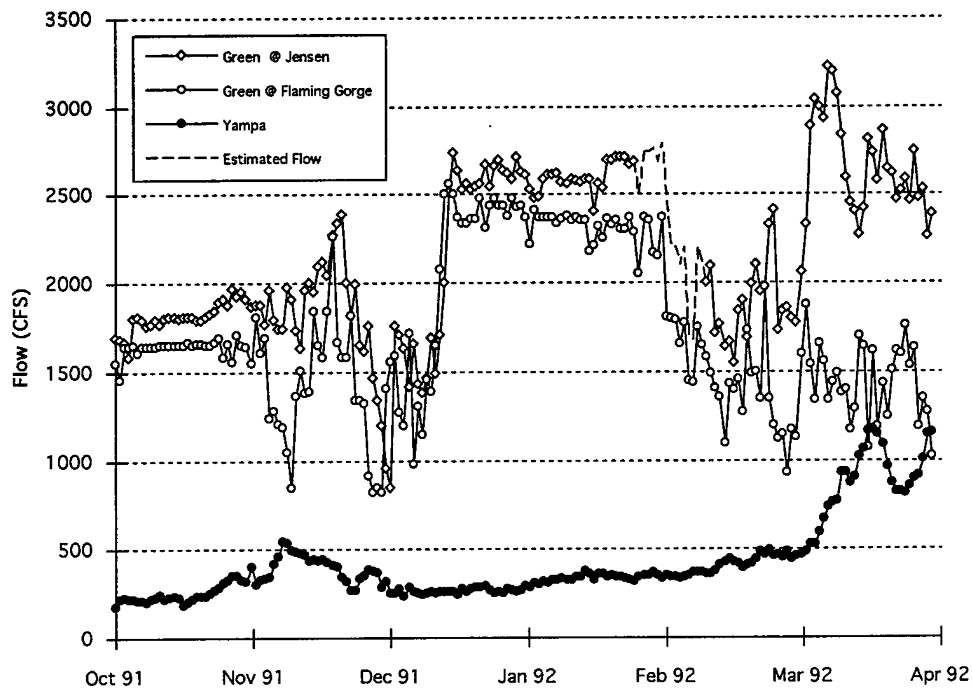

Fig. 10. Daily flows on the Green and Yampa rivers during 1991–1992 (data from U.S. Geological Survey).

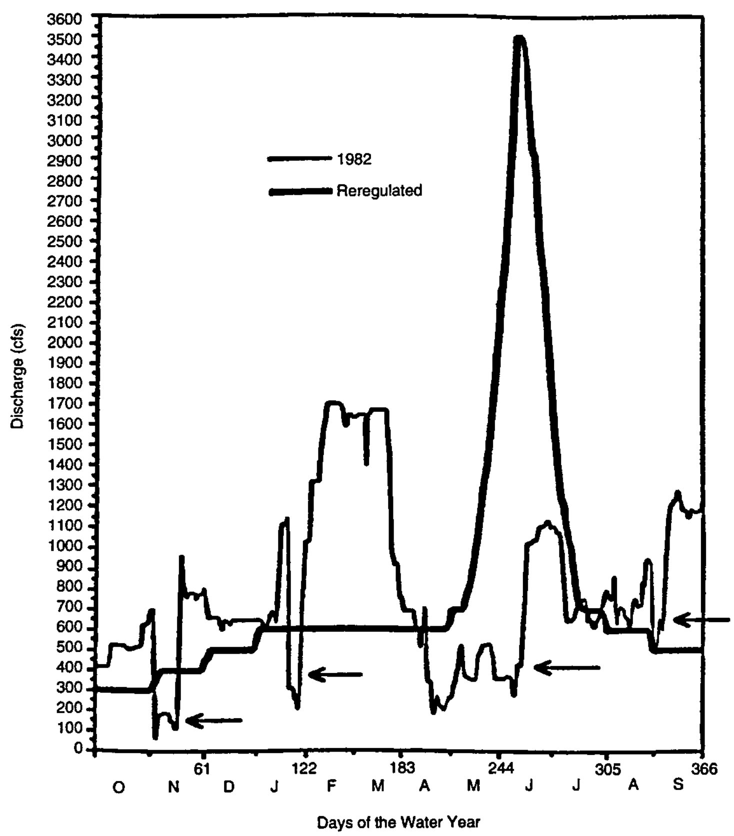

Fig. 11. Variability of flows on the Gunnison River (East Portal gauge) as a consequence of regulation by the Aspinall Units during the 1982 water year and as reregulated to simulate the predam hydrograph (from Stanford and Ward 1992b).

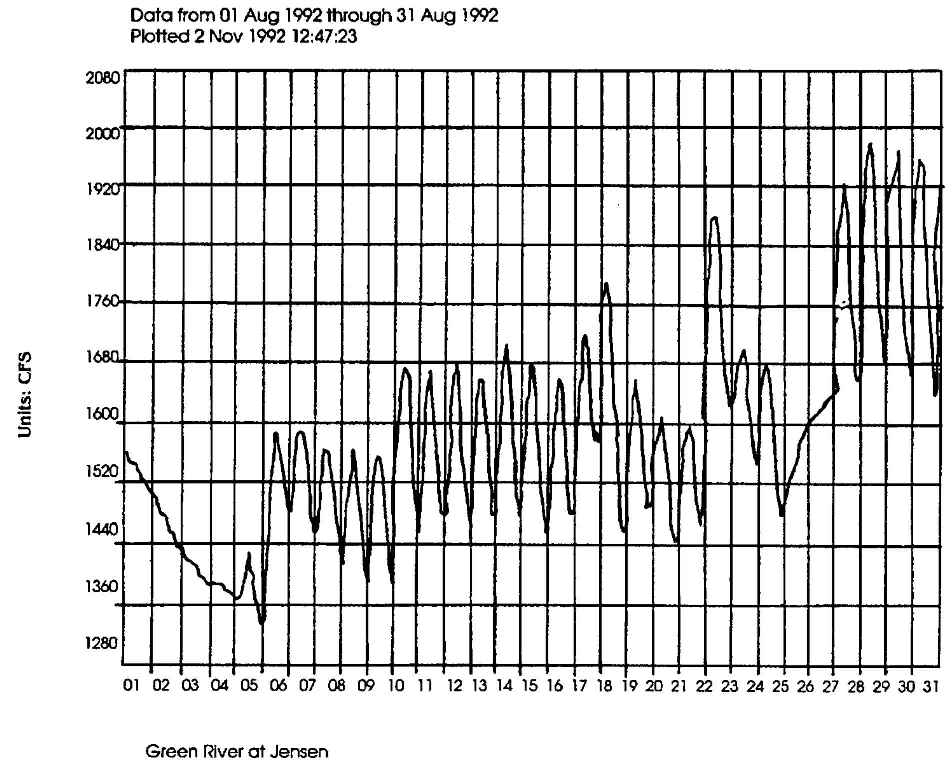

Fig. 12. Hourly discharge measured on the Green River at the Jensen gauge during August 1992. Plot provided by W. Brad Vickers (U.S. Bureau of Reclamation, Salt Lake City, Utah).

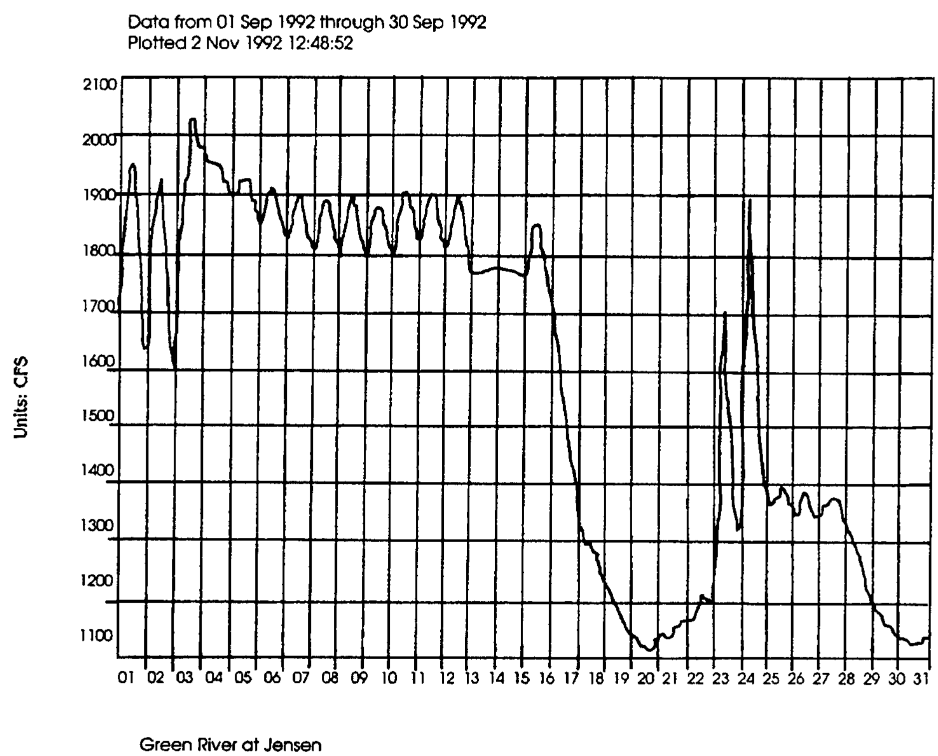

Fig. 13. Hourly discharge measured on the Green River at the Jensen gauge during September 1992. Plot provided by W. Brad Vickers (U.S. Bureau of Reclamation, Salt Lake City, Utah).

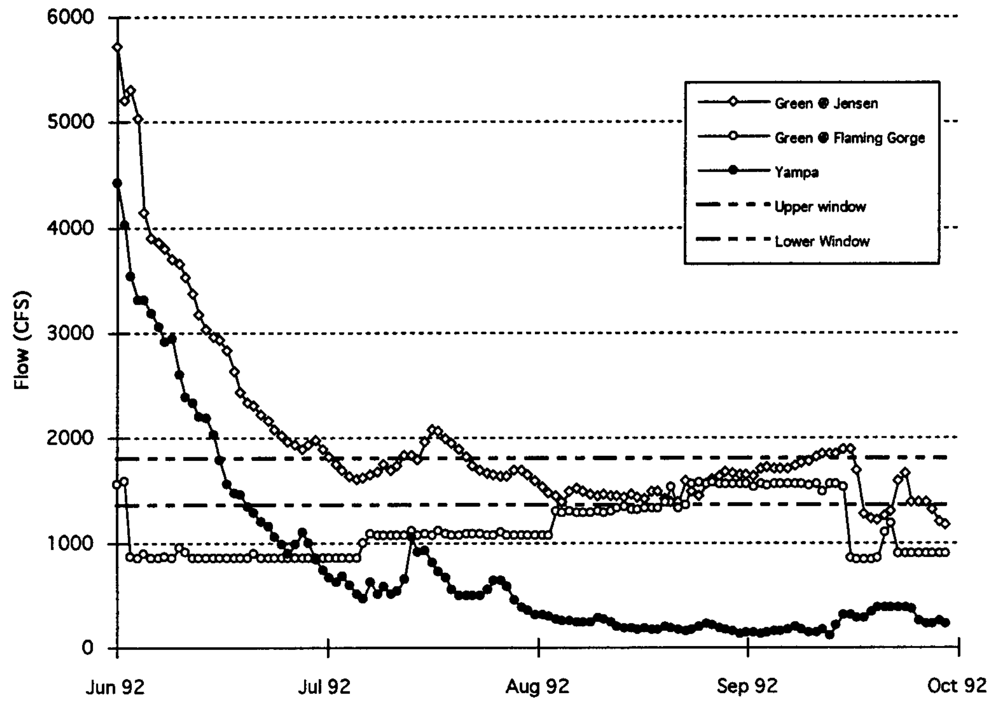

Fig. 14. Summer and fall baseflows on the Green River at Flaming Gorge Dam and at Jensen in relation to unregulated flows from the Yampa River. *Bold, broken lines* delineate 1,800 cfs (upper) and 1,350 cfs (lower) baseflow operational windows recommended for recovery of endangered fishes (U.S. Fish and Wildlife Service 1992), as derived from the stage-backwater relationship determined by Pucherelli et al. (1990) and Lyons and Pucherelli (1992) (data from U.S. Geological Survey).

substantially in over 100 years because the Yampa remains unregulated. Unvegetated, bare sandbars and backwaters evident in photographs taken in 1871 were amazingly unchanged in photos of the same spots in 1983. Record high flows in 1983 did not change this interpretation (Potter 1984). Clearly, the scouring effect of spring floods does limit the distribution of riparian plants into the channel and backwaters on the Yampa River, whereas riparian vegetation composed primarily of nonnative species such as reed canary grass (*Phalaris arundinacea*), salt cedar (*Tamarix* spp.), and Russian olive (*Elaeagnus angustifolia*) is gradually choking the regulated segments of the Upper Colorado River Basin.

Two interactive processes are involved in the long-term succession of regulated stream riparian vegetation. First, reduction of peak flows allows encroachment of riparian vegetation into the channel, backwaters, and floodplain wetlands, if the latter two are still hydrologically functional after regulation. The riparian zone of regulated rivers is small but frequently dewatered and rehydrated. Second, nonnative plants are more competitive in the stabilized environment that exists in the narrow saturated zone next to the river channel and backwaters, and they tend to dominate the community. Native plants are adapted to deal with extreme variations in flow and soil saturation, conditions that do not occur in the dynamic fashion that characterizes unregulated hydrographs in the Colorado River system. That is, in the predam environment, the riparian zone was large and only periodically or seasonally flooded. Hence, the natural plant succession that followed scouring flood events has been curtailed or lost along regulated streams, as reflected in the narrow, undisturbed riparian corridor along the wetted perimeter of the river and its backwaters (Gregory et al. 1991).

Maintenance of cottonwood (*Populus deltoides, P. fremontii*) gallery forests, which once characterized the floodplains of the pristine Upper Colorado River Basin, was dependent on seasonal flooding and drying in the riparian zone. Seeds produced by cottonwoods in spring were deposited

with debris on the floodplain surfaces as flows declined after the spring spate. Gradually drying soils of fine riverine alluvium provided ideal substratum and water supply for germination and growth of seedlings. As a result of this unique coupling of the tree's life cycle with the annual hydrograph, trees of even age can be used to date the extent of past high flow events. Moreover, cottonwood leaves dropped in fall and blown into the river provide an important allochthonous source of nutrients for riverine food webs. Only remnant forests remain today along the rivers of the Upper Colorado River Basin owing to regulation of flow, which limits distribution of seeds and conditions required for germination. Agricultural activities such as grazing and tillage, and floodplain revetments also prevent establishment of cottonwood seedlings. Replacement of riparian forests of naturally reproducing cottonwoods and associated native plants by nonnative plants in a narrow fringe along the river corridor is a classic symptom of the severing of dynamic spatial and temporal connections between the river channel and its floodplain (Stanford and Ward 1986a, 1992a, 1993).

Two questions require resolution with regard to riparian ecology and imposition of reregulated flows in the Upper Colorado River Basin. First, how much flooding and what frequency of flooding does the riparian zone require to maintain native riparian vegetation? Fisher et al. (1983) showed that the Yampa corridor remains largely unchanged, although salt cedar has invaded throughout the lower half of the river. The 1983–84 high floods allowed cottonwoods to reseed along the upper Green River (personal observation). Other flows over the last several decades have not produced cottonwoods. Second, how much of an effect will encroachment of vegetation into the river channel have on reconfiguration of the channel if peak flows are reinstated? Studies are needed to quantify this very apparent relationship between reduction of peak flow events and changes within the riparian vegetation of the Upper Colorado River Basin.

Loss of Food Web Function in the Varial Zone: The Problem of Baseflow Instability

Hydropower operations have produced erratic baseflows on the Gunnison (e.g., Fig. 11) and on the Green River (e.g., Fig. 10) that are especially problematic because they destabilize food webs in the varial zone of the river. The varial zone is the shallow area of the shoreline (as opposed to the middle or thalweg of the channel) that is inundated and dewatered by the peak flow events. Hence, the varial zone includes riparian vegetation as well as portions of the primary and secondary channels and backwaters not normally considered part of the riparian zone. In an unregulated river the varial zone may be large and dynamic in the context of natural geomorphic variability described by Fig. 2 or in the context of the gallery forest discussed above. The varial zone in a regulated river often is smaller owing to reduction in peak flows, but, more importantly, the varial zone of a regulated river usually is repeatedly watered and dewatered by dam operations for hydropower generation. As markets for hydropower vary, so does water output from the dam. The result on the Green and Gunnison rivers is reflected in high spikes above baseflow (e.g., at points of initiation shown by arrows in Fig. 11) often lasting several days (e.g., note also sudden changes in flow in Fig. 10). The extreme nature of these flow changes is more evident when hourly flows are plotted for the same periods (Figs. 12 and 13). Regulated flows below hydropower dams also often reflect the consequences of the dam operators need to control electrical load (peaking operations), as on the Green River in 1992 (i.e., diel cycles evident in Figs. 12 and 13). Peaking and other short-term operations water and dewater the varial zone of a regulated river with much greater frequency than would occur under natural conditions. Stanford and Hauer (1992) demonstrated that diel changes on the Middle Fork of the Flathead River, an unregulated snow-melt river in Montana, were consistently less than 5% per day during the baseflow period.

Repeated flushing of the varial zone prevents establishment of food webs and resting areas for small fish, which are required to support riverine fisheries. Weisberg et al. (1990) demonstrated that standing crops of zoobenthos increased 100-fold in 1 year in a regulated river after eliminating peaking operations at the dam and thereby reducing the devastating ecological effects of unnatural, short-term flushing of the varial zone. Repeated flushing also removes plant growth nutrients and alters the natural thermal insolation of shallow backwaters, which are especially important for bioproduction of low velocity food webs in general and for growth of squawfish and razorback sucker specifically.

Despite the laudable reregulation effort by operators of Flaming Gorge Dam to stay within flow

windows (Fig. 14) determined to maximize areas of backwater habitats in the alluvial nursery areas of the Green River during summer and fall 1992, peaking operations still caused considerable diel fluctuation of river stage (e.g., Figs. 12–14). I infer that backwaters thought to be protected by these flow windows were in fact flushed or, at least, significantly fluctuated repeatedly during late summer 1992. Data presented by Grabowski and Hiebert (1989) indicate that the food webs in the backwater environments of the Green River are not very productive. As noted above, these backwaters should contain rooted aquatic plants and a biodiverse, productive invertebrate and fish food web. I realize that the fluctuations shown in Figs. 12–14 are considerably reduced from operations in the past. Nonetheless, development of stable, productive food webs in the backwaters probably has not occurred as a consequence of reregulation of the Flaming Gorge releases. Moreover, these backwaters probably will never be very productive unless flow fluctuations can be eliminated. Empirical information with which to firmly judge the productivity of backwater food webs as influenced by regulated baseflow regimes throughout the Upper Colorado River Basin is sorely needed and should be approached in the dynamic time and space context described above.

Peaking operations at Flaming Gorge are attenuated in relation to distance downstream from the dam. Therefore, baseflow instability (Figs. 12 and 13) progressively worsens upstream from Jensen and may be severe in the Echo and Brown Park reaches. Elsewhere between Jensen and the dam, the river is constrained in canyons, and the problem may be somewhat ameliorated by geomorphology. However, peaking flows are known to interrupt insect emergences that feed the trout fishery in Red Canyon immediately downstream from the dam (my observation and Larry Crist, personal communication). Similar effects were observed on the Missouri River below Holter Dam in Montana, and an outcry from fly fishermen caused load control operations to be shifted to another dam. The effect was a translocation of stream regulation effects from one river to another, thereby confounding management objectives (Stanford and Hauer 1992). This illustrates the potential difficulty of changing dam operations to meet the needs of endangered fishes in potamon reaches of the Upper Colorado River Basin, if rhithron trout fisheries might be influenced in the process.

Stream Regulation Mediates Invasions of Nonnative Predators and Complicates Provision of Instream Flows to Protect Endangered Fishes

Introduction of trout and other nonnative fish in regulated streams is an enormously confounding problem in the interpretation of the ecology of regulated streams because the native species virtually always seem to decline in the presence of exotics, especially if the river is regulated. This pervasive ecological problem has been reviewed thoroughly (e.g., Mooney and Drake 1986). Predation of natives, including endangered fishes, by exotics does occur in the Upper Colorado River Basin, and red shiner, fathead minnow (*Pimephales promelas*), walleye (*Stizostedion vitreum*), northern pike (*Esox lucius Linnaeus*), channel catfish, largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieui*), and green sunfish are especially problematic invaders (cf., Karp and Tyus 1990; Tyus 1991b; Tyus and Haines 1991). However, Meffe (1984) and Minckley and Meffe (1987) showed that intense flooding in rivers in the southwestern United States was positively correlated with diversity and abundance of native fishes and negatively correlated with diversity and abundance of nonnative fishes. The strong inference is that nonnatives are maladapted to survive intense and frequent (annual, at least) flooding compared with natives. Having fewer predators increases recruitment of natives and over time allows the natives to persist in greater abundance than nonnatives (Fig. 15). The work of Meffe and Minckley included the Virgin River and other tributaries of the Colorado River but none in the upper basin. Thus, while the data are not directly applicable, the relationship probably holds. Hawkins and Nesler (1991) correlated lower ratios of nonnatives to natives with high peak flows in the Yampa River, and red shiner populations declined after years of high spring flows in the Colorado River (Osmundson and Kaeding 1991).

The prediction that flooding will limit predation mortality of endangered fishes is used as one rationale in the recovery program for reinstatement of peak flows. However, introduced species, red shiner for example, are native in rivers that experience floods (of bankfull or greater) rather frequently, which suggests that flow augmentation might not work very well in controlling some nonnative species. However, the complex interactions described above that are associated with

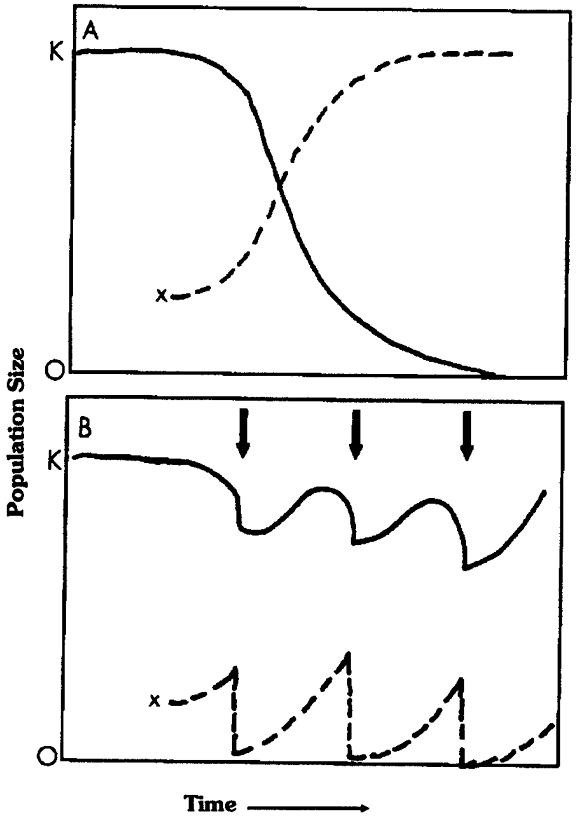

Fig. 15. Models of the dynamic relationship between native and nonnative fishes in regulated (A) and unregulated (B) arid-land streams. A: In a regulated stream native fishes (*solid line*) typically decline and disappear after introduction (x) of nonnative fishes (*dashed line*). B: In a free-flooding stream, native fishes similarly decline after nonnatives appear, but flooding (*arrows*) reduces nonnative populations to levels that permit recovery of native fishes. During interflood periods, population size and range of nonnative fishes again expand and negatively impact native species until the next flood. If flooding occurs frequently enough, long-term coexistence may occur as a dynamic equilibrium. K = carrying capacity of the stream for native fishes (from Minckley and Meffe 1987).

major disturbance events, like flooding, may not occur the same way in all rivers or all river reaches, even if they are prone to flooding. The relationship needs to be examined and compared in constrained and unconstrained reaches.

Stream Regulation in an Ecosystem Context: Occurrence of Ecological Discontinuities

The cumulative effect of regulation, especially when deep-release dams control the flow downstream, is that the rhithron-potamon transition zone is pushed downstream, producing an ecological discontinuity (sensu Ward and Stanford 1983). Biophysical conditions characteristic of headwater (rhithron) segments occur in reaches that were characterized by warmwater conditions before regulation. Very productive coldwater food webs, including stenotherms such as stoneflies and trout (Fig. 1), establish in waters that were inhabited by potamon species prior to impoundment.

Regulation of the Gunnison River by the Aspinall Units (Fig. 9) has produced a classic and well documented ecological discontinuity. The position of the rhithron-potamon transition has shifted downstream 70–80 km (Ward and Stanford 1991) as a consequence of reduced peak flows and colder water temperatures. Bankfull discharge of 11,000 cfs in the Gunnison Gorge downstream from the dams occurred every 3.2 years before regulation. Given the storage capacity of the Aspinall Units, the historical water yield of the catchment, and current regulation regime, bankfull discharge will occur only once in 40 years in the future (Elliott and Parker 1992). Moreover, baseflows are high and variable (e.g., Fig. 11) owing to hydropower operations, and the hypolimnial releases have cooled the river at the confluence of the North Fork (Fig. 1) by nearly 10° C during summer (Stanford and Ward 1983). A reproducing (wild) rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) fishery (Nehring 1988) developed in association with a biodiverse and very productive coldwater zoobenthos community from Crystal Dam through the Gunnison Gorge to below the confluence of the North Fork (Fig. 16; Hauer et al. 1989; Stanford and Ward 1989; Ward and Stanford 1990, 1991; Stanford and Ward 1992b). Hence, the rhithron-potamon transition zone, which occurred within the Gorge prior to regulation, now occurs below the North Fork confluence. Creation of this substantial ecological discontinuity, coupled with construction of the Redlands and Hartland diversion dams, which blocked migration pathways many years ago (Quartarone 1993), undoubtedly has contributed to the demise of squawfish and razorback sucker in the Gunnison River, where they were formerly abundant (Tyus 1984; Minckley et al. 1991; Tyus 1991a).

The new rhithron community in the regulated Gunnison River, however, is extremely fragile owing to the responsiveness of the ecological discontinuity to flow and temperature, as controlled by reservoir releases (Stanford 1989). Indeed, the

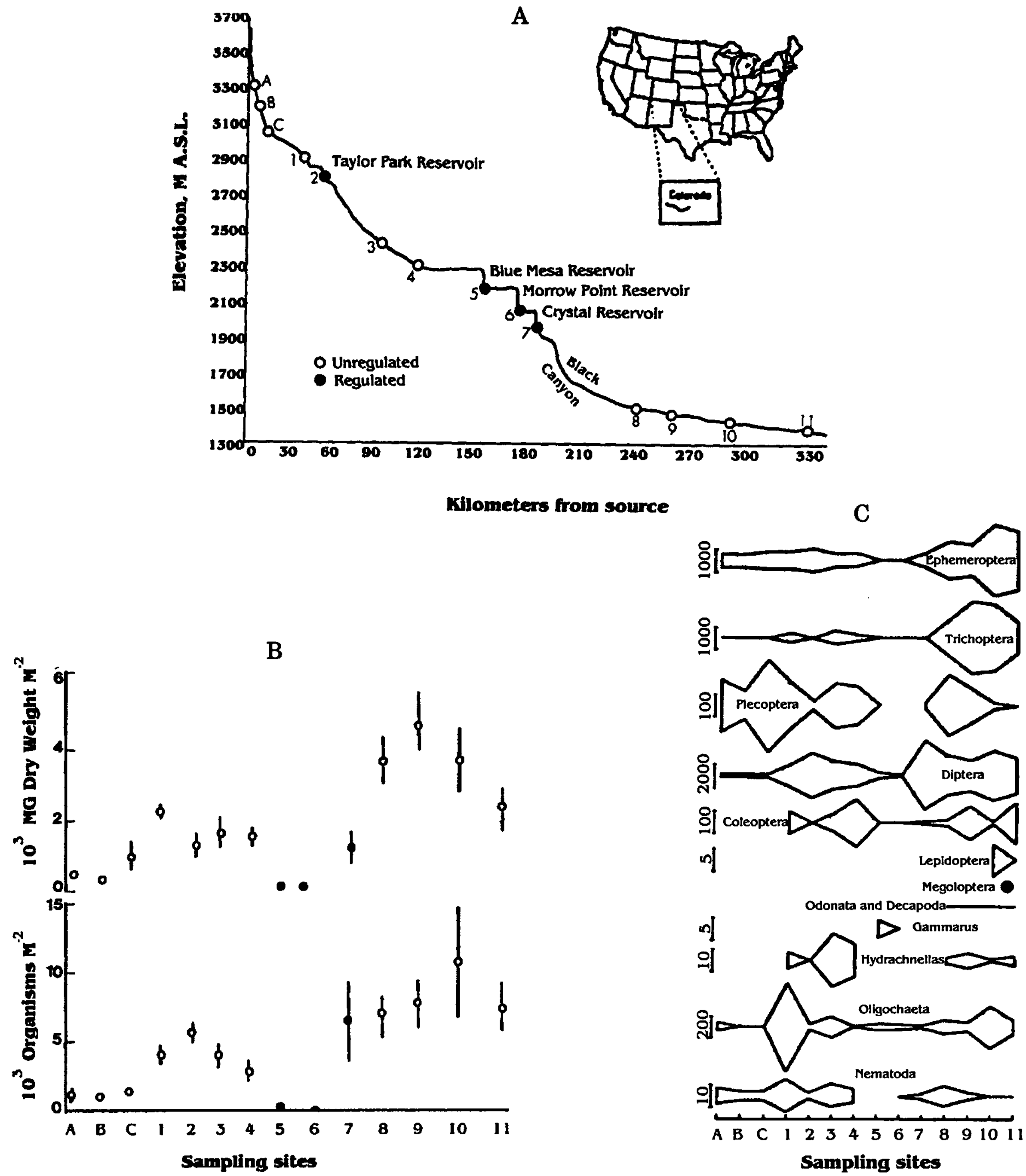

Fig. 16. A. Altitudinal profile of the Gunnison River. B. Biomass and density (mean and SE bars) of total zoobenthos in the Gunnison River from the headwaters to mouth. Sites 1–11 (located in A) were sampled in 1979–1980. C. The contribution of major groups to the total number of zoobenthos collected per site (located in A) in 1979–1980 (from Ward and Stanford 1991).

new rhithron food web, including the valuable trout fishery, was severely damaged by the episodic side flows that occurred during summer 1991 and 1992, when the regulated flows were at or near the 300 cfs minimum. Benthos and fish were smothered by fine sediments, a situation that has persisted owing to the lack of a spring flush to clean the substratum (my observation). Recent experimental flows to help determine flow recommendations for endangered fishes in the Gunnison River reached 4,000 cfs in 1992 but were insufficient to rearrange alluvium entrained in the river channel (Elliott and Parker 1992). Because of the interactive effects of (1) a lack of spring peaks or other flushing flows, (2) an extended period of minimum flow (both 1 and 2 due to drought and regulation), (3) warmer temperatures associated with low flows, and (4) episodic loading of the channel from ephemeral side flows, the position of the discontinuity moved upstream during 1991–92, and side channels and eddies filled with fine sediments and vegetation. Today, the riparian corridor of the river is densely vegetated, and surface water and groundwater exchange with critically important backwater systems (e.g., Fig. 2) has been altered or lost (Stanford and Ward 1992b). The food web in the lower part of the Gunnison Gorge remains impaired owing to persistent fine sediments in and on the substratum, which prevents establishment of a productive biofilm and restricts attachment sites for zoobenthos.

The Gunnison River case history illustrates a classic response of a stream to regulation. Similar results have been recorded elsewhere (e.g., Petts 1986; Stanford and Hauer 1992). An upstream discontinuity exists on the Colorado River (Voelz and Ward 1991) and the Green River (Pearson and Franklin 1968; Pearson et al. 1968), although the latter is significantly reset toward predam potamon conditions by the Yampa River (Annear and Neuhold 1983).

Conclusions Based on Review of the Ecological Literature Pertaining to the Endangered Fishes and the Regulation of Flow

1. The endangered fishes remain relatively rare in the Upper Colorado River Basin as a consequence of stream regulation and possibly predation and other interactions with nonnative fishes. Recruitment of adults has not been clearly demonstrated for any of the species, but age structure of squawfish suggests adult recruitment is occurring (i.e., larvae, YOY, juveniles, and adults are collected each year in the Upper Colorado River Basin, although all age classes often are not observed in the same river segments). Clear evidence for adult recruitment is lacking for the other species. In recent years gravid razorback sucker and humpback chub were collected during the spawning season at a few sites, and a few YOY were collected. Bonytail chub seem to be extirpated.
2. The distribution, relative abundance, and some important physical habitat preferences of squawfish, humpback chub, and razorback sucker (in that order) are reasonably well known (Fig. 6) and documented in peer-reviewed literature. However, only the life history of squawfish is fairly well understood. Important aspects of the life history and habitat preferences for humpback chub and razorback sucker remain to be documented. Much of what is known about the life history and population dynamics of humpback chub is based on unpublished studies in the Grand Canyon, which may or may not be relevant to the Upper Basin (e.g., no population in the Upper Basin is known to migrate into a tributary to spawn, as occurs in the Little Colorado River within the Grand Canyon; Larry Crist, personal communication). Detailed information about spawning and rearing is lacking for humpback chub and razorback sucker throughout the Upper Basin, and virtually nothing is known about bonytail chub. Moreover, accurate estimates of annual population size are problematic for all of the fishes (Tyus 1992), and mark-recapture studies using the new transponder tag technology are warranted. On the other hand, a great deal more is known about the distribution and abundance of the fishes, except bonytail chub, than is known about the influences of river hydraulics, sediment transport, and riparian controls on the food web that supports the fishes. In other words, the data on which current flow recommendations are based primarily describe the distribution and abundance of the fishes, not the ecosystem-level processes and responses that determine productivity.
3. Strong linkages between trophic (food web) and geomorphic attributes of the Upper Colorado River Basin ecosystem are variable in time and space. For example, algae (periphyton) and

zoobenthos communities are more productive on cobble bars than sand, but substratum size on river bars is highly variable as a function of the dynamic sediment transport and deposition processes that occur as the river fluctuates between peak and base flows (Fig. 2). Another example, though not well documented, is the propensity for high benthic and planktonic production in subchannels (backwaters) and floodplain wetlands that were (predam) seasonally flooded. These different, yet interactive, space and time scales that produce natural biophysical variation are the essence of the ecosystem in which the endangered fishes evolved and must be documented thoroughly.

4. Studies in the Upper Colorado River Basin indicate that flow regulation, specifically reduction of the amplitude between peak and base flows, is a likely contributor to the decline of the native fishes, but the cause and effect relationship is not simple. For example, years of regulated flows, coupled with construction of revetments, seem to have reduced the availability of backwaters and wetlands as nursery habitats that support larval and juvenile squawfish. Although extremely high flows seem to be associated with weak cohorts of Colorado River squawfish and humpback chub, occasional extreme flooding needed to maintain channel morphology and channel-floodplain interactions probably is critical for long-term survival of the fishes. Indeed, the only recent incident of successful recruitment of adult razorback sucker occurred when high flows reconnected riparian gravel pits to the mainstem Colorado River. On the other hand, squawfish recruitment can occur over a wide range of spring flows, and squawfish spawning may be much less site-specific than is indicated by the literature, or a wide range of preferred spawning conditions exists on the spawning bars where squawfish are routinely found (e.g., Cleopatra's couch bar on the Yampa, Three Fords on the Green). Presence of nonnative predators and reduced complexity of habitats needed by the different life history stages of the endangered fishes (due to severing of channel-floodplain connections and encroachment of riparian vegetation into the channel) further confound determination of cause and effect. The fundamental problem with respect to provision of flows to recover the endangered fishes is balancing the many interactive effects in a manner that will favor the native fishes over the long term (i.e., decades).
5. The life histories of the endangered fishes, as well as those of zoobenthos that also have been studied in detail, are either directly or indirectly controlled by flow magnitude and timing and the relation between flow and temperature. However, relationships between flow, channel configuration, and thermal heterogeneity (cf., Ward 1984) have not been well integrated conceptually or empirically or in the context of the various life history stages of the fishes. A squawfish life history energetics model, for example, would be very helpful in this regard.
6. Stream regulation has introduced serial discontinuities (i.e., downstream extension of coldwater or rhithron environments) within the river continua of the Upper Colorado River Basin. The location and persistence of these discontinuities are directly related to flow and largely determine where the endangered and other native fishes can achieve a positive life history energy balance (i.e., complete the life history with net recruitment of young at or above minimum viable population size). Remember, these fishes are adapted to potamon conditions, and the length of the potamon zone has decreased as a consequence of the downstream extension (discontinuity) of the rhithron zone through regulation of flow from the deep storage reservoirs. The concept of ecosystem "resets" and discontinuities (sensu Ward and Stanford 1983), coupled with the notion that connected channel and floodplain (backwaters, wetlands) components of the riverscape are seasonally pulsed by flooding (Ward 1989), robustly integrates the myriad biophysical processes that are influenced by stream regulation. Strong inferences about how a river ecosystem may respond to alternative flow management actions must be derived in this ecosystem context. The downstream shift in the position of the rhithron-potamon transition is an ecosystem-level measure of change wrought by regulation and should be used to adjust flows to maximize conditions known to be favorable to potamon (e.g., endangered fishes) and rhithron (e.g., trout) fisheries.
7. Strong food web interactions are probably occurring as a consequence of the presence of a wide variety of nonnative fishes, which now dominate fish communities throughout

the Upper Colorado River Basin. Despite demonstration of important effects of predation and competition for food resources, little information exists about the ecology of nonnatives in the Upper Colorado River Basin. High flows seem to reduce numbers of nonnative species, and diversion dams installed many years ago (e.g., Redlands on the Gunnison River) may have segregated nonnative populations and limited range expansion; however, much more information is needed. I suspect that considerable unpublished data exist in files as a consequence of the sampling effort required to collect significant numbers of the endangered fishes. If so, the information should be examined relative to what is known about the native species and published. If not, sampling protocols should be developed to describe trends in nonnative populations in all segments of the river. In addition, experiments are needed to clarify interactions between natives and nonnatives.

8. River ecosystems are too complex to be described by deterministic models or constructs of individual attributes. Ecosystem components are N-dimensional and inherently variable (stochastic), and they interact in complex ways that cannot be predicted from logistic equations. Construction of an ecosystem model that describes all of the dynamic processes discussed above is likewise unreasonable as a predictive tool. Therefore, the prudent alternative is to use all available ecological information to derive and implement a flow regime for the Upper Colorado River Basin ecosystem and to quantify variables (e.g., location of serial discontinuities, bioproduction of food webs, condition and quantity of low velocity habitats, availability of spawning habitats, spawning success, population dynamics of native and nonnative fishes) that describe whether the ecosystem is changing in a way that favors recovery of the fishes.

Derivation of Flows Currently Recommended to Protect the Endangered Fishes

Review of Instream Flow Methodology

For well over 2 decades many different researchers have toiled to derive a general (easy to use), precise (gives the same answer in repeated tries), and real (accurately describes the many interactive processes that occur in nature) model to predict stream flows to protect fish and invertebrates. Considering the myriad factors that influence the distribution and abundance of endangered fishes in the Upper Colorado River Basin, and how intractable controlling factors become when many different river systems and biota are of interest, the search for such a model is formidable. Nonetheless, instream flow modeling has been fostered by the extreme value of water and the unwillingness of water development interests to "experiment" with flows on a river-by-river or even segment-to-segment basis. Much litigation has resulted over the need to maintain flows within river segments to protect biota and channel and floodplain features at the expense of flow depletion for other human uses or at the expense of less flexibility for hydropower operations.

Flow Threshold Models

A two-volume proceedings (Orsborn and Allman 1976) of a special symposium on rationale for and approaches to instream flow methodology sponsored by the American Fisheries Society and the American Society of Civil Engineers set the stage for this endeavor to couple management-oriented aquatic science with the physical mechanics of water flow in stream channels. From the outset a fundamental tenet of the evolution of instream flow methodology was that something simpler (less mathematical) and more intuitive (to field personnel working for management agencies) than full-blown ecosystem simulation was needed. Consequently, the methodology has tended to focus on economically important fishes and their habitat "preferences," as determined by flow. This should not be surprising because a primary objective of wildlife and fisheries management for decades has been to protect and enhance species-specific habitats to maximize carrying capacity and hence maximize harvest of surplus biota.

The first widely used methods were entirely based on the fact that, below some flow threshold, physical habitat becomes limiting to fish and other stream biota during some part of their life cycle. The most commonly used method was the "Montana" method (Tennant 1975 and various modifications, see Wesche and Rechard 1980 for review), which attempts to relate perceived problems, though rarely quantified (my observation,

but also see Morhardt 1986), of the regulated flows to the historical flow regime that occurred on the average. This approach to habitat optimization, though still widely used (Reiser et al. 1989a), does not consider the importance of flow variation and its complex relation to channel geomorphology.

Statistical Approaches

Many studies have attempted, with varied success, to statistically relate some measures of the biophysical attributes of rivers and streams to the disturbance effect of flow variation. Most of these studies are basic science, where the intent was to document aspects of the structure and function of stream ecosystems with respect to flow changes. Much of the work was focused on demonstration of relationships between the distribution, abundance, and behavior of aquatic biota and important physical variables using various regression and multivariate analyses in natural (regulated situations compared with unregulated controls) and experimental designs (experimental manipulations designed to simulate flow effects; cf., Kroger 1973; Reice 1985; Perry et al. 1986, among many others). However, very few studies actually demonstrate a statistically valid relationship between biomass or some other abundance measure and flow variables that apply to different streams or even different stream segments. Morhardt (1986) reviewed and annotated 72 studies that attempted to derive a general instream flow model that would accurately predict productivity related to flow variables *in different streams*. Only one (Binns and Eiserman 1979) produced a statistically valid result, and Morhardt (1986) concluded that was because the streams were in the same region and were biophysically very similar. Armitage (1989) was able to predict the occurrence and biomass of macroinvertebrates from a suite of environmental variables using gradient analysis (TWINSPAN) in regulated streams in England. But, again, these streams are homogeneous compared with the large rivers of the Upper Colorado River Basin, and the distribution of zoobenthos in English rivers, which have been regulated for centuries, is well known. In small streams where flow processes are relatively uniform (nonstochastic) and distribution and abundance of biota are well known, relationships can be demonstrated with statistical accuracy and precision. Detailed presentations of the science of stream ecology with respect to the effects of flow and hydraulics were given by Resh et al. (1988) and Statzner et al. (1988).

In rivers that are large and complex most studies are site specific by design because unbiased replication of sites across streams is difficult, if not impossible, owing to the stochastic nature of large rivers. In fact, replication within a stream segment is difficult because flow mechanics produce so many different microhabitats that it is almost impossible to take enough samples to describe biotic distributions. Pseudoreplication is a problem in many studies. All streams are ecologically different, and therefore mechanistic models must compromise reality to gain generality. The alternative is essentially a trial and error approach. In other words, multivariate analyses may show that certain flow variables influence biotic productivity in a regulated stream; therefore, a particular flow pattern should optimize productivity. The only way to verify that prediction is to implement the flow regime and monitor productivity.

Incremental Flow Modeling

Despite the inherently variable nature of lotic ecosystems, the need to describe continuous functions between flow and habitat is widely perceived, along with the assumption that aquatic biota in rivers are primarily limited by availability of physical habitat. Physical variables, such as temperature, velocity, size of gravel, cover, and so forth, obviously vary with flow. So models were developed in an attempt to describe change in these habitat variables in increments of flow. This vastly more complicated approach still implies, incorrectly perhaps, that as habitat increases so will fish carrying capacity and hence fish populations.

By far the most used (Reiser et al. 1989a) and most sophisticated incremental method is that developed by the U.S. Fish and Wildlife Service (Bovee 1982). This method is called the Instream Flow Incremental Methodology (IFIM) and is a collection of computer programs and analytical procedures designed to predict changes in fish or invertebrate habitats in a "representative" stream reach due to flow changes. The IFIM has three major components: (1) transects across a "representative" reach are divided into cells (intervals) in which depth, velocity, cover value, and often substratum roughness or quality are measured or simulated. These variables are assumed to be independent of one another; (2) the ranges of velocities, depths, and cover or substratum used by the biota are determined by relating occurrence of various life history stages (e.g., YOY, juveniles, adults, spawners) of target species to "hydraulic" variables.

Life stages of target biota are sampled or otherwise monitored (fish preferences are often determined from animals fitted with radio transmitters) across the range of the hydraulic variables to derive "habitat suitability curves." Intuitively, this is a logical approach, but it is often biased by sampling error, especially in large, deep, and often turbid rivers, where the biota are difficult to capture or see; (3) the net suitability of use of a given locality (transect cell) is quantified by a variable called weighted usable area (WUA), which is a derived relation between plan area of the transect cell (area available) and the habitat preference indices (from suitability curves) for velocity, depth, and substratum. The WUA is calculated cell by cell and summed for the entire reach and over a range of discharges. Hence, increments of WUA for a stream become a continuous function of discharge. Easy to read and more detailed descriptions of the IFIM are given by Gore and Nestler (1988) and Nestler et al. (1989). This procedure has been widely used to justify flow provisions in regulated streams throughout North America, in some cases leading to state statutes to guarantee protection of aquatic biota (Reiser et al. 1989a).

Even though the IFIM has become an industry standard (Reiser et al. 1989a), it has a number of faults that are not widely recognized or understood within management circles. Concern exists regarding use of suitability curves as probability functions (Patten 1979; Mathur et al. 1985; Moyle and Baltz 1985); the assumption of independence of depth, velocity, and substratum (Patten 1979; Malthur et al. 1985); the lack of a demonstrated relation between WUA and a meaningful measure of productivity or biomass (Mathur et al. 1985; Bowlby and Roff 1986; Conder and Annear 1987; Scott and Shirvell 1987); and lack of any relationship with regard to many other ecosystem processes, such as predation and other density-dependent relationships, which clearly influence population structure (Moyle and Baltz 1985; Bowlby and Roff 1986; Orth 1987; Stanford and Ward 1992a). To my knowledge none of these criticisms has been resolved, nor is it likely they will be. However, these criticisms have been placed in perspective with respect to the rationale and intent of the IFIM, which is often misunderstood, misrepresented, and misused (Gore and Nestler 1988). For example, the model was not intended to predict biomass; it is a physical habitat simulator. Even when the model is applied properly, a variety of problems may emerge depending on input choices, which necessitates a clear understanding of how the model works. The simulator can use a variety of hydraulic predictors (e.g., the HEC-2 flow model of the U.S. Army Corps of Engineers), each of which has biases and therefore will result in different WUA calculations (Gan and McMahon 1990). Suitability curves not derived on site (i.e., curves given in the literature) are often used, which can also bias output (Gore and Nestler 1988).

The IFIM was used in an attempt to derive flow recommendations for specific river segments of the Upper Colorado River Basin for the endangered fishes. However, in the analysis WUA often was maximized for various life history stages of squawfish and humpback chub at very low flows that in the historical record were exceeded most or all of the time (Rose and Hann 1989). Such output is nonsense because the ecological data for these fishes clearly shows the importance of backwaters and eddies that occur at much higher flows. The problem here is that the IFIM probably should never have been used in the big river reaches of the Upper Colorado River Basin. When low velocity habitats are abundant, as they are throughout the potamon of the Colorado River system, the simulator underestimates the WUA; in fact, the model cannot deal with zero-flow habitats. This explains why the IFIM works well only in small streams where the channel is characterized by uniformly varying flow (e.g., the low velocity profile reflects steady, uniform flow, which is also an assumption of the HEC-2 hydrology simulator that is often used in IFIM; my observations). Also, habitat suitability curves were probably biased because the fish were difficult to observe or collect in the usually turbid, deep water of the Yampa and Green rivers (Rose and Hann 1989), which is precisely why the adult fish monitoring program (U.S. Fish and Wildlife Service 1987b) emphasizes shallow, shoreline habitats that can be sampled effectively by electrofishing. However, the fishes routinely use deepwater habitats (e.g., Tyus and McAda 1984; McAda and Kaeding 1991), and movement between habitats (e.g., channel, backwaters) on a diel basis cannot be accounted for in the method. The utility of the IFIM evolved a great deal during the period that data were being gathered in the Upper Colorado River Basin studies, and deficiencies in the method with regard to the Colorado River were probably not apparent at the time much of the data were gathered.

Are There Other Options?

Strong inferences can be derived from careful measures of channel processes that influence habitats important to the fishes. Reiser et al. (1989b) described the physical relationships between hydraulics and movement of sediments with respect to deriving flushing flows to remove fine sediments entrained within the bottom of an alluvial river. These principles of flow mechanics can be used to derive other formalized approaches to manage flows for the purpose of maintaining channel forms the fishes use. Sediment transport mechanics depend on detailed information on sediment gradation, channel geomorphology, and channel slope. If data needed to calculate sediment mass balance are available and are coupled with detailed topographic information, derived either from aerial photographs or surveys over the period before and after regulation, the morphological dynamics of the channel can be documented (cf., Andrews 1986; Lyons and Pucherelli 1992), and informed approaches to flow negotiations can proceed. However, regime analyses too often rely on untested assumptions that some flow volume and rate relationship, usually bankfull flow, is the dominant channel-forming flow. Determination of bankfull flow is problematic owing to local variations in channel morphology coupled with usually too few data on hydraulics of the reach during peak flow events.

In my view the preferred approach is a thorough, empirical understanding of sediment gradation, channel geomorphology, and channel slope, with which movement of sediment and hence the dynamics of many physical habitats important to aquatic biota can be estimated as a function of the amplitude of peak flow events. Andrews and Nelson (1989) used this approach to document topographic responses of a large bar complex in the Green River over a history of flow events. A major advantage of the model is that, although it is deterministic, flows, sediment supply, and, to some extent, topography can be stochastic. The model is being used to predict dynamics of sediment transport and channel topography in response to flow variation elsewhere in the Colorado River system. Model development and verification is greatly assisted by recent improvements in automated field surveying equipment (total stations) that allow rapid and very accurate measurements of local topography (E. D. Andrews, personal communication). However, as concluded by Reiser et al. (1989b), the most certain method to determine relationships between peak flow events and channel features in a regulated river is to tag an array of bed materials, carefully survey channel topography (sensu Andrews and Nelson 1989), and relate movement of materials and changes in topography to different flow events carefully controlled by reservoir releases. However, the flow peaks have to be high enough to move the tagged bed materials, which can be approximated using standard hydraulic calculations.

From a more biological perspective, several alternative approaches are possible. Binns and Eiserman (1979) predicted trout biomass in Wyoming streams with a habitat quality index (HQI) in which 11 habitat variables, including baseflow and annual change in discharge, thought to influence trout populations were rated subjectively. The predictions were significantly correlated with actual measures of biomass. The Delphi rating schedules used in this technique apparently resolved much of the nonlinearity usually observed in relationships between habitat descriptors and fish biomass. The Delphi method is an iterative procedure for obtaining consensus of best professional judgment, when direct measurements are not available (Zuboy 1981). However, Bowlby and Rolf (1986) were not as successful in using the method in Ontario streams because trout density changed within stream segments when habitat variables remained the same. Other biophysical indices of habitat quality have been proposed (cf., Osborne et al. 1992; Rabeni and Jacobson 1993); they have been used to establish relative influences of stream regulation in different streams, but to my knowledge they have not been used to examine incremental effects of flow.

A general (simple application in different streams) incremental flow-biomass model that is statistically precise (repeatable) and accurate (describes reality) is probably not attainable, especially in large rivers like the upper Colorado, where ecosystem structure and function are complex and poorly known. However, the problem can be approached from a multidisciplinary perspective, where strong inferences about how the endangered fishes are likely to respond to reregulated flow regimes can be derived from process-oriented studies that demonstrate key biophysical relationships. Linking hydrology, geomorphology, and limnology in an ecosystem context is the key (Stanford and Ward 1992a), and I recommend below a new approach for reaching an ecosystem level of understanding with respect to flow provision in potamon reaches of the Upper Colorado River Basin.

Flow Regimes Recommended to Protect and Enhance Endangered Fishes in the Upper Colorado River Basin

In this section I present flow recommendations made by the U.S. Fish and Wildlife Service, and in the following section I discuss the problems with these recommendations. Flow recommendations have not been made for the Gunnison, White, and Dolores rivers, major tributaries that have considerable potential as habitat for endangered fishes, as well as for augmenting flows in important segments of the Colorado and Green rivers.

Yampa River (U.S. Fish and Wildlife Service 1990):

- The "historical" flow pattern ("percentile flows that occur naturally"), based on a derived monthly regime that included 68,800 acre-feet depletion of historical flow, will be maintained.

Green River (U.S. Fish and Wildlife Service 1992):

- Between 1 April and 15 May releases from Flaming Gorge will ramp upward (< 400 cfs/day), corresponding to the trend measured in the Yampa. Releases from Flaming Gorge will correspond to the peak flow in the Yampa to yield flow between 13,000 and 18,000 cfs for 1 (dry year) to 4 (wet year) weeks between 15 May and 1 June. This may require release of 4,000–4,700 cfs from Flaming Gorge for the duration of the peak; if peak flow in the Yampa is < 9,000 cfs (very dry year), release from Flaming Gorge will be 4,000–4,700 cfs for 1 week, corresponding to the Yampa peak flow.
- Releases from Flaming Gorge will ramp down (< 400 cfs/day) to 2,000 cfs for at least 1 week and then to 1,100–1,800 cfs at Jensen (first gauge below the Yampa-Green confluence) by 20 June in dry years, 10 July in normal years, and 20 July in wet years (target dates can be adjusted as new information on larval drift and entrainment in nursery areas becomes available). Hourly flows at Jensen will be maintained at 1,100–1,800 cfs (±12.5%) until about 15 September; compensation for freshets from the Yampa (natural events) is not required. Water released from Flaming Gorge during this period will be from the warmest strata possible to produce temperatures in the Green River at Jensen that are no more than 5° C colder than temperatures in the Yampa at its confluence with the Green.
- From 15 September to 1 November flows will be as above, except during wet years, when a range of 1,100–2,400 cfs (±12.5%) will be allowed.
- From 1 November flows will remain stable through the ice formation and spring breakup period, except as necessary to produce storage in Flaming Gorge that will ensure spring through autumn flows given above. If ice is not present, flows may vary within constraints of the U.S. Bureau of Reclamation agreement with Utah (i.e., 800–4,700 cfs). Section 7 consultation will occur if emergency events impact Reclamations ability to comply with the above for more than 20 h during any month.
- Beginning in spring 1992 "research flows" will be allowed. These experimental flows will be used to refine the current recommended flows as per priorities annually agreed upon by the U.S. Bureau of Reclamation, U.S. Fish and Wildlife Service, and Western Area Power Administration. The effects of winter baseflow on full peaking power fluctuations will be evaluated, along with 1 year of stable winter releases at or below 2,000 cfs and 1 year of spring flows utilizing jet tube bypass at the dam. Other research concerns listed were temperature control by selective withdrawal, feasibility of retrofitting bypass tubes for generation to allow bigger spring peaks, and mechanisms of legal protection of instream flows, presumably through appropriation of conditional instream flow rights. Various studies underway in FY 93 are summarized in Bureau of Reclamation (1992) and include studies of larval drift of squawfish, razorback sucker, and humpback chub; overwinter survival of YOY squawfish; geomorphic classification and ecology of backwaters; nonnative fish management; and wetlands rehabilitation (Old Charley Wash).

Colorado River Above Confluence With the Green River (Kaeding and Osmundson 1989; Osmundson and Kaeding 1991):

- At the state line gauge:
  (1) maintain or increase the current 25% peak flows (high day of the year) at 30,000–40,000 cfs (squawfish recruitment peaks);

(2) increase the frequency of years with peak flows in excess of 40,000 cfs from 1 in 12 years (8%, the current condition) to 1 in 4 years (25%; i.e., flushing peaks); and
(3) the rest of the time (50%) maintain peak flows equal to or exceeding 22,000 cfs (minimal recruitment peak).

- Within the 15-mile reach provide peak flows as given in the Table.

Problems With the Flow Recommendations of the U.S. Fish and Wildlife Service

Yampa River

Recommendations made for the Yampa River specify maintenance of historical flows. This recommendation apparently was determined solely on the rationale that natural flows would foster continued spawning success by squawfish and increase the likelihood that remaining razorback sucker and humpback chub would be protected.

The Yampa River is a critical habitat for the endangered fishes. Recruitment of populations in the Green River may depend on spawning sites in Yampa Canyon. Most importantly, the Yampa River is the only reasonably pristine tributary remaining in the Upper Colorado River Basin. Hence, I view it as a "control" for evaluating the success or failure of interim flows adopted in the regulated reach, which will be a critical assessment to be made in the future. Therefore, I support the recommendation in principle, but the historical baseline used to derive mean monthly flows seems to be incorrect. Depletions in the Yampa River currently are about 110,000 cfs (Fig. 7; Brendecke 1993), not 68,000 cfs. Also, I do not think it is appropriate to use monthly means in such analyses because daily flow variation is a very important component of river ecology. The daily flow duration curve for the period of record would more accurately reflect the real baseline. Moreover, if natural seasonal and daily flow variations are vital to the fishes, then the natural diel and daily flow variation observed in the Yampa River should provide a basis for designing more benign flows in the regulated Green River.

Green River

Recommendations on the Green River were based on inferences from ecological studies of the endangered fish and the backwater area to discharge relationship determined by Pucherelli et al. (1990). The main intent of the peak flow recommendation by the U.S. Fish and Wildlife Service apparently was to add volume to the peak flows derived from the Yampa River to create an annual spring peak sufficient to flood and maintain connectivity of the channel to backwater environments and floodplain wetlands in the alluvial reaches near Jensen and downstream.

Rationale for duration and amplitude of the spring peak was not given except with regard to constraints on releases at Flaming Gorge Dam (i.e., only 4,000 cfs can be discharged through the generators, and an additional 4,000 cfs can be passed through bypass or jet tubes without opening flood gates). The fact that the Yampa and Green rivers historically peaked at different times was not clearly addressed, nor were the proposed ramping rates on the rising and falling limbs of the hydrograph, in either the context of the discharge to backwater area relationship of Pucherelli et al. (1990) or the need to establish ecologically functional wetlands on the floodplain (e.g., flooded bottomlands at Escalante Bottom). The 1992 spring flows followed the hydrograph recommended in the Biological Opinion (Fig. 17).

Rationale for fluctuation criteria during baseflow each year was not explicit. The intent apparently was for the Bureau of Reclamation to select a target flow between 1,800 and 1,100 cfs and not

Table. Recommendations for spring flows in the 15-mile reach (from Osmundson and Kaeding 1991).

Frequency (percent of years)	Peak day	Mean monthly discharge (cfs) April	May	June
25%	> 23,500	> 3,900	> 12,900	> 16,300
25%	20,500–23,500	3,200–3,900	10,800–12,900	12,800–16,200
50%	14,800–20,500	2,400–3,200	8,300–10,800	10,000–12,800

- Maintain July–September flows from 700 to 1,200 cfs in normal or wet years and 600 cfs minimum in dry years within the 15-mile reach.
- Maintain current (1954–1989) base (winter) and transition (October and March) flows (1,000–2,000 cfs) in the 15-mile reach

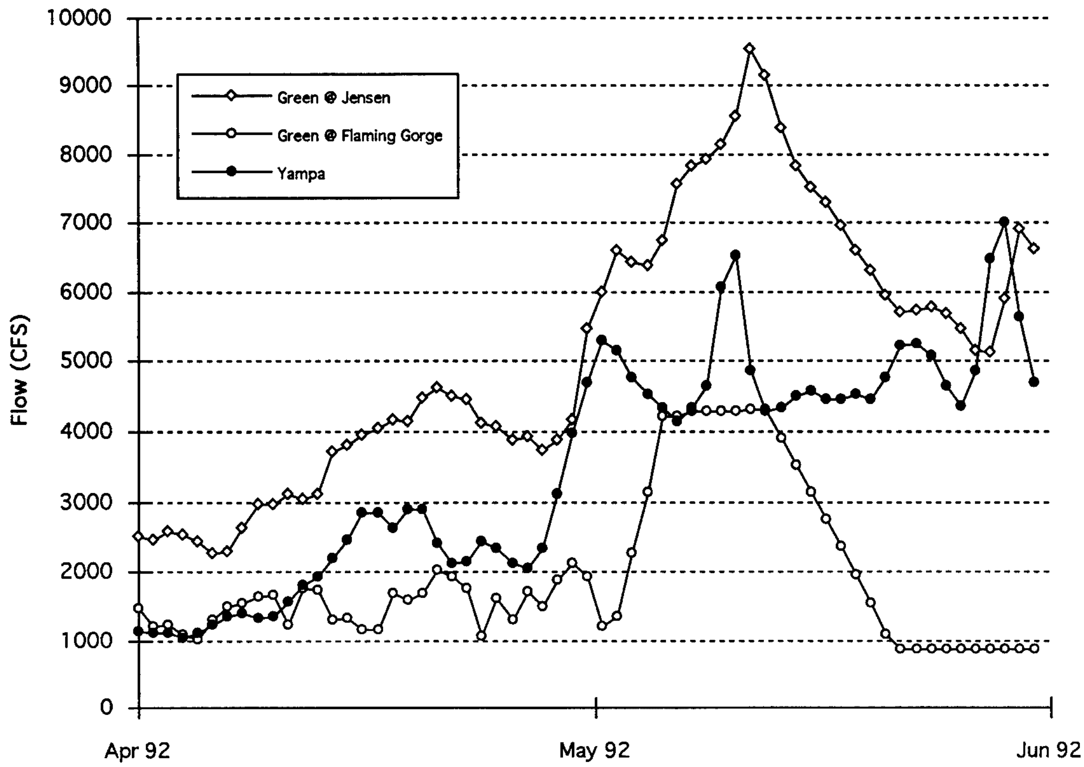

Fig. 17. Daily flows in the Green River at Flaming Gorge Dam and at Jensen in relation to unregulated flows from the Yampa River during spring 1992 (data from the U.S. Geological Survey).

vary it more that ±12.5%. The rationale for the 12.5% figure was not given. However, for perspective, flows in the North Fork of the Flathead River, Montana (an unregulated river similar in size and water yield to the Yampa and Green rivers), do not vary more than about 5% per day at baseflow and 10% per day during spring runoff (Stanford and Hauer 1992). As noted above, this relationship should be examined quantitatively on the unregulated Yampa River to shore up the fluctuation criteria for Flaming Gorge Dam operations during summer and for the duration of the baseflow period.

However, the current interim flow regime allows a great deal of fluctuation at baseflow. Due to Flaming Gorge operations, rapid and severe fluctuations were apparent in hydrographs obtained during late summer and winter 1992, (Figs. 10, 12, 13, and 14) at the Jensen gauge on the Green River downstream from the Yampa confluence. These hydrographs were recorded after the interim flow criteria described above were supposedly implemented, yet the fluctuations do not correspond to the criteria. I believe that even strict adherence to the recommended baseflow criteria of the interim flow agreement will not protect (and certainly not enhance) bioproduction and species diversity of food webs within the varial zone of the river (including backwaters and floodplain wetlands). Bioproduction in backwaters probably is virtually eliminated by one dewatering event, and some period (weeks to months) of more stable water levels may be required for recovery (my observation). Moreover, the flow-backwater relationship of Pucherelli et al. (1990), on which the baseflow recommendations were made, is valid only for current channel morphology and will probably change with the onset of new peak flows. Additional research is needed to clarify these important flow-backwater food web relationships, but it must be linked to a more predictable baseflow regime from the dam.

The ecological basis of the temperature criterion (i.e., < 5° C change at Jensen relative to Yampa River temperatures at the confluence) was not established for either the channel or the backwater environments. The temperature pattern in the channel and backwaters is critical to the ecology of the river and hence survival of the fishes. Temporal and spatial patterns of temperature in

the Green River depend on the release level at Flaming Gorge, volume, distance from the dam, ambient air temperatures, channel morphology, and amelioration effects by side flows, especially the Yampa. This relationship apparently can be partially controlled by the selective withdrawal system at the dam, at least to Jensen.

These concerns are clearly problematic with respect to legitimacy of the flow recommendations for the Green River. Some of my concerns may be resolved by the ongoing 5-year research program, although workplans I reviewed were too brief to allow judgment on that issue. Moreover, integration among projects on the Green River and with recovery projects elsewhere in the Upper Colorado River Basin is lacking or unclear. Research objectives ought to be fairly uniform throughout the Upper Basin, given that the same fishes and ecological issues are involved in all of the tributaries.

My greatest concern with recommendations for the Green River, however, is that peak flows are not very high and baseflows not very low and stable by predam standards (i.e., the ratio of peak to baseflow is 40 based on predam flows of record, whereas the recommended ratio is 12). Hence, the flow recommendations may not do much ecological good, especially if the peaks do not accomplish much channel reconfiguration, and baseflow fluctuations for hydropower operations do indeed compromise stability of the slackwater food webs.

Colorado River

On the Colorado River, the IFIM and a U.S. Fish and Wildlife Service flow-temperature model were used to predict July–September baseflows that maximized runs, riffles, and pools (not backwaters) used by adult squawfish and increased temperatures 1–2° C over 1978–86 observed values (with the thought that age-0 fish would grow faster). Discharge, backwater, and temperature relationships, therefore, may be suspect, owing to the tendency of the IFIM to overemphasize the importance of low flows as preferred habitats. The analysis may be generally correct by default because Kaeding and Osmundson (1988) argued convincingly that the 15-mile reach is thermally suboptimal habitat. Certainly, lowered summer flows should allow the water to warm up more. However, note that the recommended flows ramp down to baseflow (700–1,200 cfs) very rapidly in July to warm up the river. This could result in stranding of insects and fish and surely decrease productivity of riverine food webs. Moreover, backwaters might be too shallow to support food webs that need to be sustained. Work is underway to provide a better estimate of the flow-backwater relationship in the key reaches of the Colorado River (Doug Osmundson, personal communication). In general, the rationale for baseflows is much more refined and based on data than that of the Green River.

Spring flows on the Colorado rivers were recommended on the basis of departure from historical records and the need to flush the rivers to revitalize low velocity habitats that are thought to be critical to the survival of the fishes. I support the intent, based on my review and synthesis of the ecology of the rivers. However, the spring flow recommendations were also rationalized in part on the perceived need to provide intermediate flows 50% of the time to foster favorable recruitment of squawfish (i.e., frequency of peak flows were based on data in Fig. 4). Similar data were not presented to support this flow recommendation on the Green River, although I understand that 1983–84 cohorts were low in relation to flows of record (Tim Modde, personal communication). The flow-recruitment relationship should be thoroughly examined and presented in the context of adult captures over the long-term flow record in both rivers. I noted above my concerns with the flow-recruitment relationship of Fig. 4, but if the general relationship of Fig. 4 is valid, and I think these are pivotal data, a tradeoff exists. High flows in the Colorado River (and elsewhere) may be expected to produce in- and off-channel habitats that are critical to squawfish and razorback sucker at the expense of recruitment of squawfish. Intermediate flows may produce stronger squawfish cohorts as habitat quality in general deteriorates and may significantly decrease production of razorback cohorts because wetlands or gravel pits cannot be accessed. I think the recommended flows, if implemented as interim flows over a reasonably long (5 years) period, will allow the consequences of this tradeoff to be clarified.

Peak flows exceeded 30,000 cfs at the state line 23 out of 51 years in the period of record used to rationalize flow recommendations for the 15-mile reach, so the recommendation that high flows occur 25% of the time is somewhat confusing. According to Doug Osmundson (personal communication), this really means that at least 1 year in 4 should have peaks of 30,000–40,000 cfs, and currently, that is the case. However, peak flows at the state line gauge are due in large part (47%) to

discharge from the Gunnison River, and how that system fits into the picture is not clear. This seems problematic if different flows are ultimately derived for the Gunnison River.

Currently, squawfish population dynamics and spawning success are unknown in the Gunnison River, even though squawfish have been collected above the Redlands diversion dam. Reregulated flows and removal of the diversion dams, provision of bypass devices, or introduction of cultured stocks may allow the squawfish and razorback sucker to recover in the Gunnison River. The same applies to the Colorado River with respect to the Palisade diversion dams that delimit the upstream end of the 15-mile reach. Conditions seem very favorable for squawfish and razorback sucker upstream from diversion structures on both rivers, although temperature regimes may be on the cold side of optimum for growth and production.

Because peak flows also are needed on the Gunnison to rebuild habitat, the recommendations for the 15-mile reach may be higher than needed. Similar concerns may apply to other tributaries, especially the Dolores and White rivers. However, the flow recommendations for the Colorado River are based on more solid, rationalized data than those for the Green River. The recommended peaks and baseflows more closely reflect predam conditions despite the dramatic depletions that have occurred in the Colorado River above the Gunnison River confluence (Fig. 8).

Differing Methodologies and the Role of Professional Judgment

Because I was specifically asked to review the methods used by the U.S. Fish and Wildlife Service for assessing instream flows, the efficacy of the various instream flow methodologies apparently was not fully understood while studies leading to the recommended flows were being conducted. Heavy investment was made in the IFIM,which was not warranted. The method, as currently formulated, should not be used in the future in the potamon reaches of the Upper Colorado River Basin because of the problems I detailed above. Weaknesses in the IFIM approach were recognized as flow recommendations were developed, and the IFIM analyses were not used to support the flow recommendations on the Green and Yampa rivers. Rather, ecological data and interpretations were couched in terms of "professional judgment" to provide rationale for the recommendations. On the Colorado River, the IFIM analyses were used explicitly, along with reference to other studies (e.g., squawfish need clean gravel scoured by spring runoff and 18° –22° C temperatures, which usually occur on the declining limb of the runoff, to spawn successfully). Use of the IFIM on the Colorado River and nonuse of it on the Green River raised doubts about the recommended regimes, which undermined the clear inference from the ecological studies that higher amplitude peak to baseflow regimes were needed.

Moreover, emphasis on professional judgment was overemphasized, given the general high quality of the ecological studies that were available. I agree with Tyus (1992) that considerations of instream flow provisions were based on ecological information obtained in suboptimal habitats of these fishes. And perhaps the biological opinion process overshadowed the science.

The recommendations should have been based entirely on inferences from long-term quantifications of energetics, habitat preferences, recruitment, channel geomorphology, and food web composition and stability and simple correlations with the highly variable flows of the 1980's. Had that been done, I think the flow amplitude recommended by the U.S. Fish and Wildlife Service on the Green River would have been higher (higher spring peaks, lower baseflows) and more consistent with my synthesis of the existing information. The Colorado River recommendations probably would not be much different than were proposed because they were logically based on the available information, and model components of the IFIM were simply used to reinforce the underlying logic of those recommendations. That a high peak to baseflow ratio should be reflected in the recommended flow regimes to protect the endangered fishes is strongly implied by the available science and is not simply professional judgment. However, segmenting the ecosystem to make flow recommendations and using different approaches to similar problems in the three segments for which flow recommendations have been made clearly undermined the credibility of the science (see also University of Colorado, Denver 1993). However, ongoing work seems responsive to criticisms, and the depth of understanding and methods seem to be converging within the system. I hope this review will foster that convergence and focus attention on the larger issue of critical uncertainties with the state of the knowledge base, not just on the problems associated with some methods.

Critical Uncertainties in the Recovery Program With Respect to Provision of River Flows to Protect Endangered Fishes

In a program with a scope the size of the recovery program for endangered fishes in the Upper Colorado River Basin, uncertainties are inevitable. However, uncertainties must be recognized and confronted if program goals are to be reached. Based on my review of the ecological information and recognizing the problems in the methodological approaches that were used to derive flow recommendations to protect these fishes, several key uncertainties appear to be critical to the goal of establishing flow regimes that will recover the endangered fishes.

Critical Uncertainties at the Program (Management) Level of Organization

1. **Flow seasonality and its correlates (e.g., temperature and physical habitat) may not be the factors limiting recovery of the native fishes.** For example, food web interactions, such as predation by nonnative fishes, may be preventing recruitment of YOY in a manner that is ecologically complex but independent of flow. Or recruitment might be limited by chronic effects of selenium or some other pollutant. Given the current data, metal toxicity seems unlikely as a limiting factor, except perhaps in localized areas where concentrations are high. However, a successful management process requires careful consideration of, and planning for, unexpected alternatives. The range of management options is proportional to the quality and depth of understanding of the scientific studies of relating flow and the dynamics of endangered fish populations.
2. **Given the high societal value placed on tailwater trout fisheries and the high priority placed on meeting entitlements under the Colorado River Compact and current water law, water volume in the Colorado and Green rivers may be insufficient to produce flows required to recover the endangered fishes.** A firm, common understanding of water supply and legal allocation is required so that valid alternatives can be reasonably derived from the ecological studies. Confidence in water supply predictions is equally as important as predictions of water needed to recover the endangered fishes. Both of these issues will evolve as more information is available, so it is wise to keep them in the same context.

Critical Uncertainties at the Information (Scientific) Level of Organization

1. **Simple stage-area relationships may not describe critical aspects of channel and floodplain morphology.** Formation and maintenance of low velocity channel and backwater habitats (e.g., eddies and back-bar channels; Fig. 2) and floodplain wetlands connected to the channel via surface flow are critical for successful recruitment of YOY and juveniles of all four endangered fishes. Flushing flows are needed to scour sediment and vegetation from low velocity habitats and to remove fines entrained in cobble bars to increase benthic production. However, the tradeoff between very high peaks (near flows of record) of short duration and lower peaks of longer duration (as is now proposed) has not been examined in enough detail. Flushing flows may actually degrade the channel and further cut off backwaters and wetlands owing to the decreased sediment load caused by retention in the reservoirs. The role of interstitial flow in forming and maintaining low velocity habitats and food web dynamics has not been investigated. Given that predictive models of incremental flows, geomorphology, and bioproduction have not been forthcoming, a new approach is needed (see below).
2. **What is the tradeoff between propensity of endangered fish larvae to drift downstream and the need for high flows to maintain connectivity between the channel and backwaters and wetlands?** Larval drift seems to be tightly coupled with flow volume and availability of low velocity habitats. If peak flows are implemented that are too low to create complex channel features that retain passively drifting larvae, they may be swept out of the areas where they can mature. On the other hand, reconnection of channel-wetlands could create additional or new habitat that is favorable to nonnative predators, thereby swamping the gains made by implementing

peak flows. Remember, the observation that peak flows compromise nonnative fishes was primarily made in constrained reaches (e.g., Yampa Canyon), where refugia from the scouring effects of high flows are more limited.

3. **Can food webs reestablish in the varial zone to the extent needed to recover the endangered fishes, given the windows permitted or needed for hydropower operations?** The pervasive influence of baseflow changes is not well documented and may be the factor limiting riverine productivity. This also has direct management implications because the Bureau of Reclamation can limit peaking and load operations at Flaming Gorge and the Aspinall Units to produce more uniform flows if the payoff in more productive food webs is realized, as is predicted from experience elsewhere.
4. **Can the endangered fishes expand their range and productivity given the downstream shift in the rhithron-potamon transition zone, and is the locality of the transition zone likely to stay constant as reregulated flow regimes are implemented?** Transition zones exist on each of the main tributaries, but discontinuities in the transition zones have not been examined in detail, except on the Gunnison River. The combination of temperature and bed materials of the predam rhithron-potamon transition zones no longer seem to occur in the regulated segments. Seasonal and annual temperature patterns have shifted downstream, and sand domination of bottom substratum has shifted upstream. Understanding and predicting these shifts as a consequence of flow and temperature regulation by the dams is critical to management of the endangered fishes.
5. **Interactions with nonnative fishes may limit recovery of endangered fishes regardless of flow provisions.** During the eons that the native fishes of the Colorado River have persisted, environmental conditions, including flows, have varied considerably as climatic patterns changed. But at no time in their evolution were the native fishes faced with the pressures associated with the onslaught of fishes introduced by man during the last half century. Nonnative fishes are a major force in the future of the endangered fishes: Lessons from Lake Mohave with razorback sucker indicate that predation can completely eliminate YOY despite numbers spawned. Management options need to be listed and rationalized with respect to the possibility that higher peak flows may not control nonnatives to the extent that recovery can progress. More detailed information about the strength of interactions involving nonnatives in riverine food webs will be required.

Recommendations: An Ecosystem Approach

In a very provocative and insightful essay, Ludwig et al. (1993) contended, among other things, that effective management of natural resources requires understanding and confrontation of uncertainties, while keeping in mind that controlled and replicated experiments normally used in science to resolve cause and effect are impossible to perform in large-scale systems, that actions are often needed before scientific consensus can be achieved, and that scientists can be relied on to recognize and quantify problems but not to remedy them. I believe that each of these points is relevant to the endangered fishes problem of the Upper Colorado River Basin. Uncertainties must be confronted by obtaining additional and more comprehensive information about how the endangered fishes function in the Upper Colorado River Basin ecosystem. Regardless of our inability to firmly demonstrate population dynamics of the endangered fishes, they are rare, and further scientific study predicated on forecasting the future will not make them more abundant. In this final section of the report, I make recommendations that couple action (implementation of flow regimes) with additional study to resolve the uncertainties discussed previously. The recommendations constitute an ecosystem approach to resolution of flows needed to protect and enhance the endangered fishes of the Upper Colorado River Basin. In essence, these recommendations constitute a new and holistic instream flow methodology.

Implement Interim Flows That Reestablish Seasonality

Higher amplitude (peak to baseflow) annual flow regimes need to be implemented, monitored, and refined with respect to uncertainties about ecological effects and influences on water supply within the Upper Colorado River Basin. We need to understand how different seasonal flow patterns influence food webs, including species

composition, bioproduction, predator–prey interactions, and other response variables, from the rhithron-potamon transition zones to Lake Powell and, thereby, influence the population dynamics of the endangered fishes. This cannot be done without implementing higher peak to baseflow regimes in each of the major tributaries on an interim basis and carefully evaluating responses of the endangered fishes and important ecosystem attributes and processes on which they depend.

How much higher? Existing information indicates that the endangered fishes may be most compromised by poor availability of high quality (i.e., productive food webs dominated by native fish), low velocity habitats that occur in the alluvial reaches (e.g., generally corresponding to nursery areas in Fig. 1). Occasional flows of near record are needed to reform channel and floodplain features (e.g., bars, chute channels, backbar channels, floodplain wetlands). High amplitude flow patterns also are needed to create and maintain spawning habitats. Stable baseflows (i.e., without frequent fluctuations associated with hydropower peaking operations) are needed to promote food web bioproduction in all of these habitats.

I recommend immediate imposition of interim flows as currently proposed by the U.S. Fish and Wildlife Service, but with two major changes. First, peak flows should approach the range and frequency of preregulation events in relation to precipitation within each subbasin. In the Green River, peaks should be augmented by Yampa River flows, as recommended by the U.S. Fish and Wildlife Service. The same strategy should work in the Colorado River with respect to reregulation of the Gunnison River. If necessary, I would trade peak flow duration for historical amplitudes during spring runoff. However, ramping rates should not exceed the historical daily rates of change (e.g., as occur in the Yampa River hydrographs over the period of record). Better understanding of the effects of high flow duration is needed (e.g., as related to spawning success of endangered fishes and reconnection of floodplain wetlands) and should be an explicit part of the evaluation program for the interim flows. Second, summer and winter baseflows must be stable (baseloaded), with daily changes limited to preregulation conditions (e.g., again as reflected in the Yampa River hydrographs over the period of record, probably no more than about 5% per day and usually less). Minimum flows can be higher than occurred before regulation, as recommended by the U.S. Fish and Wildlife Service for the Green and Colorado rivers, but they must be relatively stable with respect to fluctuations caused by hydropower operations. Interim flows for the Gunnison, Dolores, and White rivers also should be implemented immediately. The Yampa River is the unregulated control for interpreting responses in the regulated tributaries and must remain freeflowing, with no further depletion of flows delivered to the critically important Yampa Canyon reach.

Higher amplitude (peak to baseflow) regimes may be implemented, yet fishes may not respond because of unanticipated biophysical interactions. For example, higher flows may cause the channel to degrade or incise in some alluvial segments owing to reduced sediment supply by reservoir storage. The Green River has reached a new quasi-equilibrium with respect to lowered peak flows and reduced sediment supply in the alluvial reaches below the confluence of the Yampa River, and bar erosion, rather than bar building, was observed after the 1992 and 1993 runoff events (Todd Crowl, Utah State University, Logan, personal communication). However, flows in 1992 and 1993 did not approach flow of record in the Green River, and bars formed in the last extreme event (1984) probably would have been eroded by intermediate flows. Moreover, extended, near-record flows on the Colorado River in 1993 did build bars, scour backwaters, and reconnect floodplain wetlands (Doug Osmundson, personal communication and my observation from aerial photographs taken before and after the event). So, is the problem one of sediment supply or lack of extreme flow events that would move significant volumes of sediment? These critical uncertainties cannot be resolved without implementing higher amplitude peak to baseflow regimes and quantitatively determining effects on channel and floodplain morphometry, riverine bioproduction, and population dynamics of endangered fishes, as well as on Colorado River Compact entitlements.

Interim flows must occur basinwide and without change in protocol for a period long enough for ecosystem responses, including population dynamics of the endangered fishes, to be statistically quantifiable, probably at least 10 years.

Provide Common Understanding of Water Availability

The magnitude of seasonal flows that can be produced annually will depend on availability of water in each subbasin. Interim flows proposed

above are predicated on the variability of water supply (e.g., very high flows are not expected to occur every year). A common understanding of water availability is needed to allow flows to be refined as new information about fish ecology, as well as new human demands, become apparent. The "Guru II" consultation process (University of Colorado, Denver 1993) considers the legal and industrial constraints on instream flows in the upper Colorado River. Results so far are encouraging, and I hope resulting policies will be responsive to the implications of this report. On the technical side, development of more accurate hydrologic models that focus on the process of water and sediment routing is critical to refinement of the flow recommendations. A good example is the compartmental model currently under development in the Gunnison River catchment by the U.S. Geological Survey (George Leavsley, Denver, Colorado, personal communication). This model uses climatic data to predict water yield and should be very useful in forecasting water availability, thereby allowing flow regimes on the Gunnison River to be refined annually.

Improve the Standardized Monitoring Program: Add a Community Ecology Perspective

Acquiring population dynamics data on rare fish in big rivers with complex channels is inherently difficult. The population variable most easily measured is age-0 squawfish; other life history stages are much less abundant and more difficult to sample. Other species of endangered fishes are rare in all life history stages. Statistical analyses of catch data, including YOY squawfish, are problematic because zero catches (e.g., empty seine hauls) are common and produce skewed frequency distributions. Nonetheless, the standardized monitoring program (U.S. Fish and Wildlife Service 1987b), which has been in use for over a decade, seems to effectively sample habitats that the different life history stages of squawfish, razorback sucker, and humpback chub are known to use. Standardized, long-term efforts to monitor population dynamics of the endangered fishes are essential and must be continued as a performance check on the recovery program in general, as well as for providing vital data with which to evaluate effectiveness of interim flows. However, the data should be examined by several different biometricians to increase confidence in data analyses.

Achieving more accurate population estimates by permanently tagging a large proportion of endangered fishes seems to be a priority associated with the standardized monitoring program. Passive integrated transponder tags (PIT tags, 11 mm) have proven effective and should continue to be used. New, smaller tags may soon be available to allow very small fish to be permanently tagged. However, systematic procedures are needed to ensure that tags are properly implanted in all new fish captured and that data are accurately recorded by all biologists working in the Upper Colorado River Basin. Proper mark and recapture study designs should be used, preferably after consultation with fishery biometricians who specialize in estimation of population size (e.g., Kenneth Burnham, Colorado State University). Standardized mark and recapture procedures should be formally integrated into the standardized monitoring program.

Other native and nonnative fishes also are supposed to be enumerated in the backwater seining part of the standardized monitoring program, but these data do not appear to be routinely reported or synthesized, even though nonnatives are often the most abundant fishes in samples. Much greater attention should be given to population structure of the entire community of fishes found in the backwater monitoring program so that interactions with the natives may be better understood and experiments devised to demonstrate cause and effect (e.g., predation in relation to backwater fertility). Strong inferences about the potential for recovering endangered fishes may be derived from population dynamics of other native species. Natives, including flannelmouth sucker, bluehead sucker, speckled dace *Rhinichthys osculus*, and roundtail chub, also habitually segregate within the various river segments and may be declining in areas where the interactive effects of regulated flows are most pervasive (my observation).

Data gathered to date strongly indicate that future evaluations of flow-related effects and other aspects of the recovery program should be framed from a full community ecology perspective that, of course, emphasizes the endangered fishes. Total community stability, colonization-extinction relations, trophic cascades, strong interactions, and other determinations of dynamics in the community properties of food web theory have been discussed in the literature (e.g., Lowe-McConnell 1987; Matthews and Heins 1987; Kitchell 1992) but do not seem to be part of the recovery program.

Current studies are too focused on populations of individual species instead of on the assemblages of all fish species as the key ecosystem component of the recovery program.

My studies with J. V. Ward on zoobenthos demonstrate the utility of understanding the distribution and abundance of zoobenthos species throughout the river continuum. Presence of populations of the mayfly *Traverella albertana* and the dobsonfly *Corydalus cornutus* indicate the existence of healthy potamon food webs. The salmonfly *Pteronarcys californica* is a firm indicator of the downstream end of the rhithron (Ward et al. 1986; Ward and Stanford 1991; Ward 1992). These insects are easily recognized and will be present in kick samples on clean cobble runs and riffles. If they are not present, something is probably wrong with the food web, which probably affects the endangered fishes as well. In other words, examination of other components of the food web may provide management options that cannot be derived by monitoring population dynamics of only the endangered fishes.

The standardized monitoring program can be improved by adding protocols that include data (numbers, condition, gut contents) on all of the fishes taken with different gear in each of the monitoring habitats. Quality control checks (for example, by releasing tagged fishes and invertebrates within the sampling zone and determining percent recovery) should be part of the standard protocol. This will help resolve concerns about how to handle such things as skewed distributions of various species and zero catches. Rapid assays of the prey base in backwaters and riffles (e.g., presence or absence of indicator species of zoobenthos) should also be developed; however, key elements are analysis and synthesis. These data must be accurately summarized (e.g., by demonstrating variation), examined for trends over appropriate space and time scales, and related (e.g., using multivariate statistics: Gelwick 1990; Gelwick and Matthews 1992) to other aspects of the river ecosystem (e.g., dynamics of flow, geomorphology, temperature, and other flow-related variables) on a defined schedule. I recommend that raw data and statistical summaries be reported annually so that inconsistencies with sampling protocol and responses to quality control checks can be made. On at least a tri-annual schedule, data should be appended to information collected during all previous years, examined for statistically valid trends in relation to other biophysical variables, discussed, and rationalized in a community ecology context.

Daily flow data routinely collected by the U.S. Geological Survey are critical and must be continued at all current sites. The data are needed to allow flow patterns in the major tributaries and mainstem segments in the Upper Colorado River Basin to be examined in context with biological data collected under the recovery program. Each of these sites should be reporting temperature data as well, owing to the very important interactions among reservoir release depth, distance from dams and tributaries, flow volume, temperature, and distribution of biota.

Diversify the Research Program to Resolve Critical Uncertainties

The standardized monitoring program, as described previously, should provide important spatial and temporal data to assist in evaluating and refining interim flows. However, research is needed to augment monitoring data and to address critical uncertainties with respect to flow regimes.

Research is a formal component of the recovery program; most research has focused on the distribution, abundance, and behavior of the endangered fishes. Investigations are continuing because much about these uniquely adapted fishes remains to be learned (e.g., spawning behavior of razorback sucker and humpback chub). However, the main conclusion of this report is that resolution of uncertainties with respect to flow requires a greater understanding of the coupling of physical processes associated with flow and riverine bioproduction, including floodplain wetlands. To further this understanding, several specific reaches that include a full range of geomorphic components (complex channels, bars, backwaters, and *connected* floodplain wetlands) within the continua of the Green and Colorado rivers need to be selected, and responses to the interim flows must be documented in detail.

I recommend reaches be selected within alluvial segments because a greater range of habitats occurs in association with larger floodplain surfaces, and the area of the varial zone is larger than in the canyons. Moreover, refining flows for the alluvial segments probably will produce favorable results (not necessarily optimal) in the constrained reaches of the system. Sites known to be important to the endangered fishes should be emphasized (e.g., Cleopatra's Couch Bar on the Yampa, Ouray Reach on the Green, complex channel areas above and below the Gunnison confluence in the Grand Valley, Camel Switch area on the Gunnison, and at least

one lower river site on the Colorado and Green rivers).

The modeling approach of Andrews and Nelson (1989) should be used to establish topographic and substratum changes in the study reaches as flows vary. Discharge measurements must be made on site to calibrate U.S. Geological Survey gauges to the site as input to the topographical model and for other interpretations. At some point the model should be expanded to include analysis of interstitial flow, with respect to discharge variation that occurs on short (daily to weekly) and long (seasonal and interannual) time scales.

The study reaches, and perhaps the entire river system, should be periodically stereo-photographed (e.g., after, not during, every near-record flow event) to document changes in geomorphic features and to allow inferences at the local study sites to be related to changes observed systemwide. This is also a good way to document changes in the riparian communities and nonflow sources of environmental change, such as revetments. Technology is rapidly approaching the point that near real-time data (e.g., using low altitude, multispectral video imaging, time lapse photography) may provide a better approach to regionalizing locally derived (ground-truthed) data. Currently, however, stereo photography is the state-of-the-art.

Reaches need to be instrumented with multiple temperature sensors in the various habitats (thalweg, shoreline, backwaters, air, hyporheic zone, wetlands). Small, waterproof temperature sensors with data logging microchips that are programmable and can store months of hourly data are now available to allow temperature monitoring in all habitats.

Distribution and abundance of zoobenthos (cf., Ward and Stanford 1991), zooplankton (backwaters; Wetzel and Likens 1979), and fish (all species; cf., Gelwick 1990; Gelwick and Matthews 1992; Meador and Matthews 1992) should be stratified within the reach, as determined by the diversity of detailed topographical features. These measures should complement the standardized monitoring program. Emphasis should be given to understanding backwater and wetland food webs and relationships to discharge-mediated connectivity with the river channel. Estimates of some measure of the primary producer community (e.g., organic matter standing crop in size fractions, community P/R, chlorophyll, macrophyte diversity, dry-weight biomass), also stratified within the reach, should be made in relation to at least pre- and post-spate conditions.

Interactions of flow and biophysical variables between and within reaches should be examined using appropriate statistical designs planned. Experimental manipulations should be used to verify inferences derived from time-series measures within the study reaches. For example, concern exists about backwater productivity and baseflow fluctuations. Some backwaters could be experimentally manipulated (see Box) so that stronger inferences could be derived from results obtained over time in backwaters naturally influenced by interim flows. Modeling exercises also can be insightful. Enough information exists to begin development of a life history energetics model for squawfish, which could be used to more clearly understand how the species uses its environment. A spatial and temporal model of flow volume and temperature also would be insightful in interpreting invertebrate and fish distribution data.

The approach recommended here involves expertise in geomorphology, hydrology, and fisheries;

Field Experiment on Backwater Conditions

Question: How can bioproductivity of backwater food webs be limiting to endangered fishes, when backwaters often contain many other fishes (i.e., the non-endangered fishes seem to be doing very well on whatever food resources are available)?

Hypothesis: Survival, growth, and recruitment (to maturity) of juvenile Colorado River squawfish are influenced by (1) productivity of backwaters as determined by flow fluctuations, (2) competition with other fishes for food resources, and (3) predation.

Design: 3×2 ANOVA involving *productivity* (fluctuated, stable), *competition* (among squawfish, between squawfish and nonnatives) for food and space, and *predation* (no nonnative predators, many). After consultation with a statistician to confirm the experimental design, dike and divide a large, natural backwater in such a way that one-half can be fluctuated (to simulate hydropower operations) and one-half can be kept full (to simulate a stable baseflow). Sub-divide each half with pens that can be stocked with the various combinations of squawfish juveniles (from hatchery stock) and nonnative competitors and predators.

Response variables: squawfish growth rates (e.g., daily rates from otoliths, C^{14}-labeled glycene uptake), survival, condition (e.g., liver-somatic ratio, histology).

biometrics expertise should always be a priority. The general working hypothesis is that implementation of interim flows will reestablish natural attributes and functions, especially geomorphic properties that influence bioproduction, of the Upper Colorado River Basin ecosystem and allow gradual recovery of Colorado River squawfish, razorback sucker, and humpback chub populations. Bonytail chub probably will have to be reestablished from cultured stocks.

This research plan is insufficiently detailed and needs to be tailored to the recovery program, based on a better understanding of field conditions, sampling logistics, and funding. My intent was to provide a framework for evaluating interim flows and for resolving uncertainties associated with those flows. I do not think more research has to be done before flow regimes can be implemented. On the contrary, the interim flows I identified have a good chance of having a positive effect on the endangered fishes. Simply monitoring the fishes will not provide the understanding of processes and responses that will be needed to refine the flows to the greatest benefit of the fishes while preserving other uses of the river system.

Implement a Peer Review Process

Research currently conducted as a part of the recovery program covers a gamut of objectives. Some of the ongoing work seems responsive to the implications and recommendations of this report. For example, multidisciplinary (Todd Crowl, Jack Schmidt, and others, Utah State University, Logan, working cooperatively with Leo Lentsch, Department of Natural Resources, Salt Lake City) research is being done on the Green River to evaluate aggradation and formation of low velocity habitats (using the modeling approach recommended above) with respect to recent flows, biophysical characterization of squawfish nursery habitats, and predation effects of nonnative fishes on YOY squawfish. On the Colorado River, quantification of food webs on gravel bars known to be used by squawfish and razorback sucker (using zoobenthos and community respiration or P/R measures recommended above) has been initiated (Doug Osmundson, personal communication). However, the research program in general seems segregated by foci on the Green and Colorado rivers rather than on the system as a whole, and research workplans are not very detailed, making evaluations of scientific merit difficult.

I recommend that this report be used to integrate research efforts into a systematic evaluation of interim flows in the Upper Colorado River Basin ecosystem and that a peer review process be implemented to evaluate and improve the science of projects funded by the recovery program. The recovery program should fund a panel of three to six experts (not currently associated with the recovery program) to evaluate annual research proposals with respect to program goals, scientific rationale, methods, and deliverables and to make recommendations to appropriate committees of the recovery program and the U.S. Fish and Wildlife Service. This will require that more detailed proposals be prepared, perhaps following the format of the National Science Foundation, and include a section on past performance with respect to analyzing data and publication. Publication of research results is fundamental to the peer review process. The context of the review process should be responsive to the general need to know whether the proposed projects have a high probability of resolving uncertainties concerning the effectiveness of interim flows in recovering the endangered fishes.

Implement Adaptive Management

An effective management process must be in place if managers are to respond adaptively to the implications from monitoring and research. Scientists can be relied on to identify and quantify problems with respect to the interim flows but not to remedy them. Managers must be prepared to implement an alternative regime if monitoring indicates that current flows are failing to protect the endangered fishes or are jeopardizing water development entitlements. The draft recovery implementation action plan (RIPRAP: U.S. Fish and Wildlife Service 1993) may provide the needed management umbrella. However, the conceptual foundation for interim flows and procedures by which those flows will be evaluated needs to be clearly understood by the management team. Risks and uncertainties, technical and nontechnical, also must be clearly in focus, along with alternative flow options. Moreover, other issues of importance to recovery exist that were not addressed here (e.g., feasibility of removing diversion dams or providing fish passage around them, removal of revetments to reconnect floodplain wetlands with the channel, supplementation of natural populations with hatchery stocks). Managers must ensure that such ancillary issues are considered in

the interim flow evaluation process. Above all, an ecosystem perspective must be the guidepost for recovering the endangered fishes.

I appreciate the idealism in my recommendations, and I am not convinced that existing entitlements can be developed and at the same time maintain adequately high-amplitude peak to baseflow regimes needed to recover the endangered fishes. However, my recommendations formalize the elements and measures that are critically needed to evaluate interim flows. Perhaps with better empirical information about flow effects on ecosystem attributes that critically influence the endangered fishes, parties in contention can find middle ground. However, the interim flows, evaluation procedures, and an adaptive management process need unambiguous endorsement to be successful. Although I have pointed out major differences in the data regarding the basic environmental requirements of the endangered fishes, I am satisfied that the state of the ecological knowledge in the Upper Colorado River Basin is sufficient to justify endorsement of interim flows. I am also satisfied that technical expertise exists within the recovery program or is available at research universities or among experienced consultants in the basin to resolve uncertainties associated with my interim flow recommendation. Success or failure of interim flows will be judged by long-term trends in the populations of the endangered fishes.

Cited Literature

Andrews, E. D. 1986. Downstream effects of Flaming Gorge Reservoir on the Green River, Colorado and Utah. Geological Society of America Bulletin 97:1012–1023.

Andrews, E. D., and J. M. Nelson. 1989. Topographic response of a bar in the Green River, Utah to variation in discharge. Pages 463–485 *in* S. Ikeda and G. Parker, editors. River meandering. American Geophysical Union, Washington, D.C.

Annear, T. C. 1980. A characterization of Yampa and Green River ecosystems. M.S. thesis, Utah State University, Logan. 143 pp.

Annear, T. C., and J. M. Neuhold. 1983. Characterization of Yampa and Green River ecosystems: A systems approach to aquatic resource management. Pages 181–192 *in* V.D. Adams and V. A. Lamarra, editors. Aquatic resources management of the Colorado River ecosystem. Ann Arbor Science, Ann Arbor, Mich.

Armitage, P. D. 1989. The application of a classification and prediction technique based on macroinvertebrates to assess the effects of river regulation. Pages 267–293 *in* J. A. Gore and G. E. Petts, editors. Alternatives in regulated river management. CRC Press, Boca Raton, Fla.

Binns, A., and F. Eiserman. 1979. Quantification of fluvial trout habitat in Wyoming. Transactions of the American Fisheries Society 108:215–228.

Black, T., and R. V. Bulkley. 1985. Preferred temperature of yearling Colorado squawfish. Southwestern Naturalist 30(1):95–100.

Bovee, K. D. 1982. A guide to stream habitat analysis using the Instream Flow Incremental Methodology. Instream Flow Information Paper 12, FWS/OBS-82/26. U.S. Fish and Wildlife Service, Washington, D.C. 248 pp.

Bowlby, J. N., and J. C. Roff. 1986. Trout biomass and habitat relationships in southern Ontario streams. Transactions of the American Fisheries Society 115:503–514.

Brendecke, C. M. 1993. Yampa River basin alternatives feasibility study final report. Submitted to Colorado River Water Conservation District by Hydrosphere Resource Consultants, Boulder, Colo. 270 pp.

Bulkley, R. V., and R. Pimentel. 1983. Temperature preference and avoidance by adult razorback sucker. Transactions of the American Fisheries Society 112:601–607.

Bureau of Reclamation. 1992. Recovery implementation program: Flaming Gorge five-year research program, FY 1993. U.S. Bureau of Reclamation, U.S. Fish and Wildlife Service, Utah Division of Wildlife, Larval Fish Lab (CSU), Western Area Power Admin., and Colorado Division of Wildlife, Colo. 36 pp.

Carlson, C. A., and R. T. Muth. 1989. The Colorado River: Lifeline of the American Southwest. Pages 220–239 *in* D. P. Dodge, editor. Proceedings of the international large river symposium. Canadian Special Publication of Fisheries and Aquatic Sciences 106.

Carter, J., and V. Lamarra. 1983. An ecosystem approach to environmental management. Pages 261–287 *in* V. D. Adams and V. A. Lamarra, editors. Aquatic resources management of the Colorado River ecosystem. Ann Arbor Science, Ann Arbor, Mich.

Conder, A. L., and T. C. Annear. 1987. Test of weighted usable area estimates derived from a PHABSIM model for instream flow studies on trout streams. North American Journal of Fisheries Management 7:339–350.

Craig, J. F., and J. B. Kemper. 1987. Regulated streams: Advances in ecology. Plenum Press, New York. 431 pp.

Dolan, R., A. Howard, and D. Trimble. 1978. Structural control of the rapids and pools of the Colorado River in the Grand Canyon. Science 202:629–631.

Elliott, J. G., and R. S. Parker. 1992. Potential climate-change effects on bed-material entrainment, the Gunnison Gorge, Colorado. American Water Resources Association, Reno, Nev. 9 pp.

Fisher, N. T., M. S. Toll, A. C. Cully, and L. D. Potter. 1983. Vegetation along Green and Yampa rivers, and response to fluctuating water levels, Dinosaur National Monument. Final report, Contract CX-1200-2-B024. Biology Department, University of New Mexico, Albuquerque. 179 pp.

Gan, K., and T. McMahon. 1990. Variability of results from the use of PHABSIM in estimating habitat area. Regulated Rivers: Research and Management 5:233–239.

Gelwick, F. P. 1990. Longitudinal and temporal comparisons of riffle and pool fish assemblages in a northeastern Oklahoma Ozark stream. Copia 1990(4):1072–1082.

Gelwick, F. P., and W. J. Matthews. 1992. Effects of an algivorous minnow on temperate stream ecosystem properties. Ecology 74(5):1630–1645.

Gore, J. A., and J. M. Nestler. 1988. Instream flow studies in perspective. Regulated Rivers: Research and Management 2:93–101.

Gore, J. A., and G. E. Petts, editors. 1989. Alternatives in regulated river management. CRC Press, Boca Raton, Fla. 344 pp.

Grabowski, S. J., and S. D. Hiebert. 1989. Some aspects of trophic interactions in selected backwaters and the main channel of the Green River, Utah. Final report. Bureau of Reclamation, Denver, Colo.

Graf, W. L. 1978. Fluvial adjustments to the spread of tamarisk in the Colorado Plateau region. Geological Society of America Bulletin 89:1491–1501.

Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. BioScience 41(8):540–551.

Hamman, R. L. 1981. Spawning and culture of Colorado squawfish in raceways. Progressive Fish-Culturist 43(4):173–177.

Hamman, R. L. 1985. Induced spawning of hatchery-reared razorback sucker. Progressive Fish-Culturist 47(3):187–189.

Harvey, M. D., R. A. Mussetter, and E. J. Wick. 1993. A physical process biological-response model for spawning habitat formation for the endangered Colorado squawfish. Rivers 4(2):114–131.

Hauer, F. R., J. A. Stanford, and J. V. Ward. 1989. Serial discontinuities in a Rocky Mountain river. II. Distribution and abundance of Trichoptera. Regulated Rivers: Research and Management 3:177–182.

Hawkins, J. A., and T. P. Nesler. 1991. Nonnative fishes of the Upper Colorado River Basin: An issue paper. Colorado State University and Colorado Division of Wildlife, Fort Collins. 72 pp.

Haynes, C. M., T. A. Lytle, E. J. Wick, and R. T. Muth. 1984. Larval Colorado squawfish (*Ptychochielus lucius* Girard) in the Upper Colorado River Basin, Colorado, 1979–1981. Southwestern Naturalist 29(1):21–33.

Illies, J., and L. Botosaneanu. 1963. Problemes et methodes de la classification et de la zonation ecologique des eaux courantes, considerees surtout du point de vue faunistique. Mitteilungen der Internationalen Vereinigung fr Theoreticshe und Angewandte Limnologie 12:1–57.

Inslee, T. D. 1982. Spawning and hatching of the razorback sucker *Xyrauchen texanus*. Proceedings of the Western Association of Fish and Wildlife Agencies 62:421–432.

Johnson, J. E., and B. L. Jensen. 1991. Hatcheries for endangered freshwater fishes. Pages 199–217 *in* W. L. Minckley and J. E. Deacon, editors. Battle against extinction: Native fish management in the American West. University of Arizona Press, Tucson.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. Pages 110–127 *in* D. P. Dodge, editor. Proceedings of the international large river symposium. Canadian Special Publication of Fisheries and Aquatic Sciences 106.

Kaeding, L. R., B. D. Burdick, P. A. Schrader, and W. R. Noonan. 1986. Recent capture of a bonytail chub (*Gila elegans*) and observations on this nearly extinct cyprinid from the Colorado River. Copeia 1986(4):1021–1023.

Kaeding, L. R., B. D. Burdick, P. A. Schrader, and C. W. McAda. 1990. Temporal and spatial relations between the spawning of humpback chub and roundtail chub in the Upper Colorado River. Transactions of the American Fisheries Society 119:135–144.

Kaeding, L. R., and D. B. Osmundson. 1988. Interaction of slow growth and increased early-life mortality: An hypothesis on the decline of Colorado squawfish in the upstream regions of its historic range. Environmental Biology of Fishes 22(4):287–298.

Kaeding, L. R., and D. B. Osmundson. 1989. Biologically defensible flow recommendations for the maintenance and enhancement of Colorado squawfish habitat in the '15-Mile' reach of the Upper Colorado River during July, August and September. U.S. Fish and Wildlife Service, Grand Junction, Colo. 169 pp.

Kaeding, L. R., and M. A. Zimmerman. 1983. Life history and ecology of the humpback chub in the Little Colorado and Colorado rivers of the Grand Canyon. Transactions of the American Fisheries Society 112:577–594.

Karp, C. A., and H. M. Tyus. 1990. Behavioral interactions between young Colorado squawfish and six fish species. Copeia 1990(1):25–34.

Kitchell, J. F., editor. 1992. Food web management: A case study of Lake Mendota. Springer-Verlag, New York. 553 pp.

Kroger, R. L. 1973. Biological effects of fluctuating water levels in the Snake River, Grand Teton National Park, Wyoming. American Midland Naturalist 89(2):478–481.

Lanigan, S. H., and H. M. Tyus. 1989. Population size and status of razorback sucker in the Green River basin, Utah and Colorado. North American Journal of Fisheries Management 9:68–73.

Lillehammer, A., and S. J. Saltveit. 1984. Regulated rivers. Oslo University Press, Norway. 540 pp.

Lowe-McConnell, R. H. 1987. Ecological studies in tropical fish communities. Cambridge University Press, Cambridge, England. 382 pp.

Ludwig, D., R. Hillborn, and C. Walters. 1993. Uncertainty, resource exploitation and conservation: Lessons from history. Science 260:17, 36.

Lyons, J. K., and M. J. Pucherelli. 1992. Sediment transport and channel characteristics of a sand-bed portion of the Green River below Flaming Gorge Dam, Utah, USA. Regulated Rivers: Research and Management 7:219–232.

Magnuson, J. J. 1990. Long-term ecological research and the invisible present. BioScience 40:495–501.

Marsh, P. C. 1985. Effect of incubation temperature on survival of embryos of native Colorado River fishes. Southwestern Naturalist 30(1):129–140.

Marsh, P. C., and D. R. Langhorst. 1988. Feeding and fate of wild larval razorback sucker. Environmental Biology of Fishes 21(1):59–67.

Marsh, P. C., and W. L. Minckley. 1989. Observations on recruitment and ecology of razorback sucker: Lower Colorado River, Arizona-California-Nevada. Great Basin Naturalist 49:71–78.

Mathur, D., W. H. Bason, E. J. Purdy Jr., and C. A. Silver. 1985. A critique of the instream flow incremental methodology. Canadian Journal of Fisheries and Aquatic Sciences 42:825.

Matthews, W. J., and D. C. Heins, editors. 1987. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman. 310 pp.

McAda, C. W., and L. R. Kaeding. 1989. Relations between maximum-annual river discharge and the relative abundance of age-0 Colorado squawfish and other fishes in the Upper Colorado River. U.S. Fish and Wildlife Service, Grand Junction, Colo. 25 pp.

McAda, C. W., and L. R. Kaeding. 1991. Movements of adult Colorado squawfish during the spawning season in the Upper Colorado River. Transactions of the American Fisheries Society 120:339–345.

McAda, C. W., and R. S. Wydoski. 1980. The razorback sucker, *Xyrauchen texanus*, in the Upper Colorado River Basin, 1974–1976. U.S. Fish and Wildlife Service, Washington, D.C. 15 pp.

Meador, M. R., and W. J. Matthews. 1992. Spatial and temporal patterns in fish assemblage structure of an intermittent Texas stream. American Midland Naturalist 127(1):106–114.

Meffe, G. E. 1984. Effects of abiotic disturbance on coexistence of predator-prey fish species. Ecology 65:1524–1534.

Minckley, W. L. 1973. Fishes of Arizona. Arizona Game and Fish Department, Phoenix. 293 pp.

Minckley, W. L., P. C. Marsh, J. E. Brooks, J. E. Johnson, and B. L. Jensen. 1991. Management toward recovery of the razorback sucker. Pages 303–357 *in* W. L. Minckley and J. E. Deacon, editors. Battle against extinction: Native fish management in the American West. University of Arizona Press, Tucson.

Minckley, W. L., and G. K. Mefee. 1987. Differential selection by flooding in stream-fish communities of the arid American southwest. Pages 93–104 *in* W. J. Matthews and D. C. Heins, editors. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

Mooney, H. A., and J. A. Drake, editors. 1986. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York.

Morhardt, E. J. 1986. Instream flow methodologies. Research Project 2194-2, Electric Power Research Institute. EA Engineering, Science and Technology, Inc., Research Project 2194-2. Electric Power Research Institute, Palo Alto, Calif. 176 pp.

Moyle, P. B., and D. M. Baltz. 1985. Microhabitat use by an assemblage of California stream fishes: Developing criteria for instream flow determinations. Transactions of the American Fisheries Society 114:695.

Nehring, R. B. 1988. Fisherman use and catch estimates for the Black Canyon of the Gunnison River (east portal access area below Crystal Dam to the North Fork confluence) 1988 and sport fish population analysis, 1981–1988. U.S. Department of the Interior, Bureau of Reclamation, Grand Junction, Colo. 29 pp.

Nesler, T. P., R. T. Muth, and A. F. Wasowicz. 1988. Evidence for baseline flow spikes as spawning cues for Colorado squawfish in the Yampa River, Colorado. American Fisheries Society Symposium 5:68–79.

Nestler, J. M., R. T. Milhous, and J. B. Layzer. 1989. Instream habitat modeling techniques. Pages. 295–315 *in* J. A. Gore and G. E. Petts, editors. Alternatives in regulated river management. CRC Press, Boca Raton, Fla.

Orth, D. J. 1987. Ecological considerations in the development and applications of instream flow-habitat models. Regulated Rivers: Research and Management 1:171–181.

Orsborn, J. F., and C. H. Allman, editors. 1976. Proceedings of the symposium and specialty conference on instream flow needs. American Fisheries Society, Bethesda, Md. 551 pp.

Osborne, P. L., S. L. Kohler, P. B. Bayley, D. M. Day, W. A. Bertrand, M. J. Wiley, and R. Sauer. 1992. Influences of stream location in a drainage network on the index of biotic integrity. Transactions of the American Fisheries Society 121:635–643.

Osmundson, D. B., and L. R. Kaeding. 1989. Studies of Colorado squawfish and razorback sucker use of the '15-Mile Reach' of the Upper Colorado River as part of conservation measures for the Green Mountain and Ruedi Reservoir water sales. U.S. Fish and Wildlife Service, Grand Junction, Colo. 85 pp.

Osmundson, D. B., and L. R. Kaeding. 1991. Recommendations for flows in the 15-Mile Reach during

October–June for maintenance and enhancement of endangered fish populations in the upper Colorado River. U.S. Fish and Wildlife Service, Grand Junction, Colo. 82 pp.

Papoulias, D., and W. L. Minckley. 1992. Effects of food availability on survival and growth of larval razorback sucker in ponds. Transactions of the American Fisheries Society 121:340–355.

Patten, B. D. 1979. Summary report of module B: Instream flow criteria modeling workshop. Colorado State University, Fort Collins, Colo., Experiment Station IS No. 40.

Pearson, W. D., and D. R. Franklin. 1968. Some factors affecting drift rates of *Baetis* and Simuliidae in a large river. Ecology 49(1):75–81.

Pearson, W. D., R. H. Kramer, and D. R. Franklin. 1968. Macroinvertebrates in the Green River below Flaming Gorge Dam, 1964–65 and 1967. Proceedings of the Utah Academy of Sciences 45(1):148–167.

Perry, S. A., W. B. Perry, and J. A. Stanford. 1986. Effects of stream regulation on density, growth and emergence of two mayflies (Ephemeroptera: Ephemerellidae) and a caddisfly (Trichoptera: Hydropsychidae) in two Rocky Mountain rivers (USA). Canadian Journal of Zoology 64:656–666.

Petrere, Jr., M. 1991. Life strategies of some long-distance migratory catfish in relation to hydroelectric dams in the Amazon Basin. Biological Conservation 55:339–345.

Petts, G. E. 1984. Impounded rivers: Perspectives for ecological management. John Wiley & Sons, Chichester, England. 326 pp.

Petts, G. E. 1986. Time-scales for ecological change in regulated rivers. *In* J. F. Craig and J. B. Kemper, editors. Advances in regulated stream ecology. Plenum Press, New York.

Potter, L. D. 1984. Report on the impact of the 1984 floodwaters on the vegetation of the Yampa River, Dinosaur National Monument, for National Park Service. 8 pp.

Pucherelli, M. J., R. C. Clark, and R. D. Williams. 1990. Mapping backwater habitat on the Green River as related to the operation of Flaming Gorge Dam using remote sensing and GIS. R-90-18. U.S. Bureau of Reclamation, Denver, Colo. 11 pp.

Quartarone, F. 1993. Historical accounts of upper basin endangered fish. Upper Colorado River Fishery Project. U.S. Fish and Wildlife Service, Denver, Colo. 67 pp.

Rabeni, C. F., and R. B. Jacobson. 1993. The importance of fluvial hydraulics to fish-habitat restoration in low-gradient alluvial streams. Freshwater Biology 29:211–220.

Reice, S. R. 1985. Experimental disturbance and the maintenance of species diversity in a stream community. Oecologia 67:90–97.

Reiser, D. W., T. A. Wesche, and C. Estes. 1989a. Status of instream flow legislation and practices in North America. Fisheries 14(2):22–29.

Reiser, D. W., M. P. Ramey, and T. A. Wesche. 1989b. Flushing flows. Pages 91–135 *in* J.A. Gore and G. E. Petts, editors. Alternatives in regulated river management. CRC Press, Boca Raton, Fla.

Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society 7:433–455.

Rose, K. L., and D. R. Hann. 1989. A summary of historic habitat modeling on the Yampa River using the physical habitat simulation system. U.S. Fish and Wildlife Service, Grand Junction, Colo. 18 pp.

Scott, D., and C. S. Shirvell. 1987. A critique of the instream flow incremental methodology with observations of flow determination in New Zealand. Pages 27–43 *in* B. Kemper and J. F. Craig, editors. Regulated streams: Advances in ecology. Plenum Press, New York.

Stanford, J. A. 1989. Flow alteration and ecosystem stability in the Gunnison River, Colorado: A perspective. Open File Report 105-89. Flathead Lake Biological Station, The University of Montana, Polson. 8 pp.

Stanford, J. A., and F. R. Hauer. 1992. Mitigating the impacts of stream and lake regulation in the Flathead River catchment, Montana, USA: An ecosystem perspective. Aquatic Conservation 2:35–63.

Stanford, J. A., and J. V. Ward. 1983. The effects of mainstream dams on physicochemistry of the Gunnison River, Colorado. Pages 43–56 *in* V. D. Adams and V. A. Lamarra, editors. Aquatic resources management of the Colorado River Ecosystem. Ann Arbor Science, Ann Arbor, Mich.

Stanford, J. A., and J. V. Ward. 1984. The effects of regulation on the limnology of the Gunnison River: A North American case history. Pages 467–480 *in* A. Lillehammer and S. J. Saltveit, editors. Regulated rivers. Oslo University Press, Norway.

Stanford, J. A., and J. V. Ward. 1986a. The Colorado River system. Pages 353–374 *in* B. R. Davies and K. F. Walker, editors. The ecology of river systems. Dr. W. Junk Publishers, Dordrecht, The Netherlands.

Stanford, J. A., and J. V. Ward. 1986b. Fish of the Colorado system. Pages 385–402 *in* B. R. Davies and K. F. Walker, editors. The ecology of river systems. Dr. W. Junk Publishers, Dordrecht, The Netherlands.

Stanford, J. A., and J. V. Ward. 1989. Serial discontinuities in a Rocky Mountain river. I. Distribution and abundance of Plecoptera. Regulated Rivers: Research and Management 3:169–175.

Stanford, J. A., and J. V. Ward. 1992a. Management of aquatic resources in large catchments: Recognizing interactions between ecosystem connectivity and environmental disturbance. Pages 91–124 *in* R. J.

Naiman, editor. Watershed management. Springer-Verlag, New York.

Stanford, J. A., and J. V. Ward. 1992b. Occurrence and significance of hyporheic zones in the Black Canyon of the Gunnison River, Colorado. Draft report to the National Park Service by Flathead Lake Biological Station, The University of Montana, Polson. 33 pp.

Stanford, J. A., and J. V. Ward. 1993. An ecosystem perspective of alluvial rivers: Connectivity and the hyporheic corridor. Journal of the North American Benthological Society 12(1):48–60.

Statzner, B., J. A. Gore, and V. H. Resh. 1988. Hydraulic stream ecology: Observed patterns and potential applications. Journal of the North American Benthological Society 7(4):307–360.

Stephens, D. W., B. Waddell, L. A. Peltz, and J. B. Miller. 1992. Detailed study of selenium and selected elements in water, bottom sediment and biota associated with irrigation drainage in the Middle Green River Basin, Utah, 1988–90. Water-Resources Investigations Report 92-4084. U.S. Geological Survey, Salt Lake City, Utah. 164 pp.

Tennant, D. L. 1975. Instream flow regimens for fish, wildlife, recreation and related environmental resources. U.S. Fish and Wildlife Service, Billings, Mont. 30 pp.

Tyus, H. M. 1984. Loss of stream passage as a factor in the decline of the endangered Colorado squawfish. Pages 138–144 *in* Issues and technology in the management of impacted western wildlife. Proceedings of a national symposium. Thorne Ecological Institute Technical Publication 14, Boulder, Colo.

Tyus, H. M. 1987. Distribution, reproduction and habitat use of the razorback sucker in the Green River, Utah, 1979–1986. Transactions of the American Fisheries Society 116:111–116.

Tyus, H. M. 1990. Potamodromy and reproduction of Colorado squawfish in the Green River Basin, Colorado and Utah. Transactions of the American Fisheries Society 119:1035–1047.

Tyus, H. M. 1991a. Ecology and management of Colorado squawfish. Pages 379–402 *in* W. L. Minckley and J. E. Deacon, editors. Battle against extinction: Native fish management in the American West. University of Arizona Press, Tucson.

Tyus, H. M. 1991b. Movements and habitat use of young Colorado squawfish in the Green River, Utah. Journal of Freshwater Ecology 6:43–51.

Tyus, H. M. 1992. An instream flow philosophy for recovering endangered Colorado River fishes. Rivers 3(1):27–36.

Tyus, H. M., and G. B. Haines. 1991. Distribution, habitat use and growth of age-0 Colorado squawfish in the Green River Basin, Colorado and Utah. Transactions of the American Fisheries Society 120:79–89.

Tyus, H. M., R. L. Jones, and L. M. Trinca. 1987. Green River rare and endangered fish studies, 1982–1985. Final report. Colorado River Fishes Monitoring Project, U.S. Fish and Wildlife Service, Vernal, Utah. 117 pp.

Tyus, H. M., and C. A. Karp. 1989. Habitat use and streamflow needs of rare and endangered fishes, Yampa River, Colorado. U.S. Fish and Wildlife Service, Washington, D.C. 27 pp.

Tyus, H. M., and C. A. Karp. 1991. Habitat use and streamflow needs of rare and endangered fishes, Green River, Utah. U.S. Fish and Wildlife Service, Flaming Gorge Studies Program, Vernal, Utah. 54 pp.

Tyus, H. M., and C. W. McAda. 1984. Migration, movements and habitat preferences of Colorado squawfish, *Ptychocheilus lucius*, in the Green, White and Yampa rivers, Colorado and Utah. Southwestern Naturalist 29(3):289–299.

U.S. Fish and Wildlife Service. 1987a. Recovery implementation program for endangered fish species in the Upper Colorado River Basin. U.S. Fish and Wildlife Service, Denver, Colo. 82 pp.

U.S. Fish and Wildlife Service. 1987b. Interagency standardized monitoring program handbook. U.S. Fish and Wildlife Service in cooperation with Colorado Division of Wildlife, Utah Division of Wildlife Resources, and Bureau of Reclamation, Grand Junction, Colo. 41 pp.

U.S. Fish and Wildlife Service. 1990. Streamflow needs of rare and endangered fishes: Yampa River interim flow recommendations. U.S. Fish and Wildlife Service, Denver, Colo. 13 pp.

U.S. Fish and Wildlife Service. 1992. U.S. Fish and Wildlife Service draft biological opinion on the operation of Flaming Gorge Dam. U.S. Fish and Wildlife Service, Denver, Colo. 45 pp.

U.S. Fish and Wildlife Service. 1993. Draft recovery implementation program recovery action plan (RIPRAP). Recovery implementation program for endangered fish species in the upper Colorado River Basin, Denver, Colo. 38 pp.

University of Colorado at Denver, Center for Public-Private Sector Cooperation. 1993. Recommendations on the legal, policy and institutional issues related to instream flow protection in Colorado. Prepared for the Water Acquisition Committee of the Recovery Implementation Program, Denver, Colo. 25 pp.

Valdez, R. A., P. D. Holden, and T. B. Hardy. 1990. Habitat suitability index curves for humpback chub of the Upper Colorado River Basin. Rivers 1(1):31–42.

Valdez, R. A., and E. J. Wick. 1983. Natural vs. manmade backwaters as native fish habitat. Pages 519–536 *in* V. D. Adams and V. A. Lamarra, editors. Aquatic resources management of the Colorado River ecosystem. Ann Arbor Science, Ann Arbor, Mich.

Voelz, N. J., and J. V. Ward. 1991. Biotic responses along the recovery gradient of a regulated stream. Canadian Journal of Fisheries and Aquatic Sciences 48:2477–2490.

Ward, J. V. 1984. Stream regulation of the upper Colorado River: Channel configuration and thermal heterogeneity. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 22:1862–1866.

Ward, J. V. 1989. Riverine-wetland interactions. Pages 385–400 *in* R. R. Sharitz and J. W. Gibbons, editors. Freshwater wetlands and wildlife. D.O.E. Symposium Series # 61, Oak Ridge, Tenn.

Ward, J. V. 1992. Aquatic insect ecology: 1. Biology and habitat. Vol. 1. John Wiley & Sons, New York. 438 pp.

Ward, J. V., and J. A. Stanford. 1979. The ecology of regulated streams. Plenum Press, New York. 398 pp.

Ward, J. V., and J. A. Stanford. 1983. The serial discontinuity concept of lotic ecosystems. Pages 29–42 *in* T. D. I. Fontaine and S. M. Bartell, editors. Dynamics of lotic ecosystems. Ann Arbor Science Publishers, Ann Arbor, Mich.

Ward, J. V., and J. A. Stanford. 1989. Riverine ecosystems: The influence of man on catchment dynamics and fish ecology. Pages 56–64 *in* D. P. Dodge, editor. Proceedings of the international large river symposium. Canadian Special Publication of Fisheries and Aquatic Sciences 106.

Ward, J. V., and J. A. Stanford. 1990. Ephemeroptera of the Gunnison River, Colorado, U.S.A. Pages 215–22 *in* I. C. Campbell, editor. Mayflies and stoneflies. Kluwer Academic Publishers.

Ward, J. V., and J. A. Stanford. 1991. Benthic faunal patterns along the longitudinal gradient of a Rocky Mountain river system. Verhandlungen der Internationalen Vereinigung fr Theoretische und Angewandte Limnologie 24(5):3087–3094.

Ward, J. V., H. J. Zimmermann, and L. D. Cline. 1986. Lotic zoobenthos of the Colorado system. Pages 403–423 *in* B. R. Davies and K. F. Walker, editors. The ecology of river systems. Monographiae Biologicae. Dr. W. Junk, Dordrecht, The Netherlands.

Weisberg, S. B., A. J. Janicki, J. Gerritsen, and H. T. Wilson. 1990. Enhancement of benthic macroinvertebrates by minimum flow from a hydroelectric dam. Regulated Rivers: Research and Management 5:265–277.

Welcomme, R. L. 1979. Fisheries ecology of floodplain rivers. Longman, London, England. 317 pp.

Wesche, T. A., and P. A. Rechard. 1980. A summary of instream flow methods for fisheries and related research needs. Eisenhower Consortium for Western Environmental Forestry Research Bulletin 9.

Wetzel, R. G., and G. E. Likens. 1979. Limnological analysis. W. B. Saunders, Philadelphia, Penn. 357 pp.

Wick, E. J. 1991. River management and habitat restoration strategy: An issue paper on habitat development, recovery program for the endangered fishes of the Upper Colorado. Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, Colo. 72 pp.

Wick, E. J., C. W. McAda, and R. V. Bulkley. 1982. Life history and prospects for recovery of the razorback sucker. Pages 120–126 *in* W. H. Miller, H. M. Tyus, and C. A. Carlson, editors. Fishes of the upper Colorado River system: Present and future. Western Division, American Fisheries Society, Bethesda, Md.

Wick, E. J., D. L. Stoneburner, and J. A. Haeking. 1983. Observations on the ecology of Colorado squawfish in the Yampa River, Colorado, 1982. Water Resources Field Support Lab, Fort Collins, Colo. 55 pp.

Wydoski, R. S., and J. Hamill. 1991. Evolution of a cooperative recovery program for endangered fishes in the upper Colorado River basin. Pages 123–135 *in* W. L. Minckley and J. E. Deacon, editors. Battle against extinction: Native fish management in the American West. University of Arizona Press, Tucson.

Zuboy, J. R. 1981. A new tool for fishery managers: The Delphi technique. North American Journal of Fisheries Management 1:55–59.

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